

Status of Pollinators in North America

Committee on the Status of Pollinators in North America, National Research Council

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STATUS OF POLLINATORS IN NORTH AMERICA

Committee on the Status of Pollinators in North America

Board on Life Sciences
Board on Agriculture and Natural Resources
Division on Earth and Life Studies

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Preface

The magnitude and direction of all manner of anthropogenic global environmental change have lately come to dominate the national conversation: at the movies, on the Internet, and in the press. Entering the term “environmental crisis” on Google generates close to 52 million hits, and the debate is raging over the validity of various projections of consequences and diverse proposals for remediation. Of the multitude of ways humans could be harming the planet, however, one that has largely been ignored is the “pollinator crisis”—the perceived global decline in the number and viability of animal species that facilitate reproduction of flowering plants, the overwhelming majority of plants in terrestrial communities. In her hugely influential book *Silent Spring* published more than 40 years ago, Rachel Carson recognized the central role of pollinators. They are the proverbial birds and the bees, along with many other insect species and even a handful of mammals, that maintain human health and terrestrial biodiversity. Carson painted a bleak picture of a world with “fruitless falls.” In the intervening decades, reports have quietly accumulated from virtually every continent of shortages or extinction of pollinators of various descriptions.

Ironically, despite its apparent lack of marquee appeal, pollinator decline is one form of global change that actually does have credible potential to alter the shape and structure of the terrestrial world. Over the past decade, the public has begun to take notice and ask whether a pollinator crisis is brewing and, if so, what can be done to avert it. The National Research Council, in keeping with its charter to provide independent, objective analysis and advice on scientific matters of national importance, took on this issue at the request of the U.S. Department of Agriculture and the U.S.

Geological Survey and commissioned a study; overseeing the study process were the Board on Agriculture and Natural Resources and the Board on Life Sciences.

Because the efforts of pollination are so pervasive ecologically and economically, the committee charged with assessing the status of pollinators required representation of a breadth of interests and abilities. The 15 members came from across the United States, Canada, and Mexico, and their expertise encompasses ecology, population biology, ethology, genetics, evolutionary biology, botany, entomology, systematics, agricultural economics, apiculture, and conservation biology (Appendix A). The committee devoted more than a year to examining literature, meeting with the experts who are most familiar with the lives of pollinators, and meeting with people whose livelihoods depend on pollinator activities. Evonne Tang, Senior Program Officer for the Board of Life Sciences, labored brilliantly and tirelessly to arrange meetings, secure information, make contacts, and reconcile and edit numerous versions of the report. Fran Sharples, Director of the Board on Life Sciences, was generous with administrative, scientific, and moral support. From the Board on Agriculture and Natural Resources, Robin Schoen, director; Karen Imhof, administrative assistant; and Peggy Tsai, research associate, provided invaluable guidance, organizational effort, and logistical assistance in support of the project.

It seems particularly appropriate that a study examining the health and well-being of the premier ecological mutualism on the planet should result from mutual respect and cooperation among a group of dedicated scholars. That the conclusions reached by the committee and presented in this report will inspire a rash of Hollywood disaster films is extremely unlikely—tidal waves, floods, fires, and explosions still remain inherently more cinematic than just about anything involving flowers, birds, bees, and butterflies—but it is to be hoped that the recommendations will inspire discussion and action nonetheless.

May Berenbaum
Chair, Committee on the Status of
Pollinators in North America

Acknowledgments

This report is a product of the cooperation and contributions of many people. The members of the committee thank all of the speakers who attended its first committee meeting on July 6, 2005, the workshop on October 18–19, 2005, and the third committee meeting on January 14, 2006 and others who provided information and input. (Appendix B presents a list of presentations to the committee.)

This report has been reviewed in draft form by persons chosen for their diverse perspectives and technical expertise in accordance with procedures approved by the National Research Council's Report Review Committee. The purpose of this independent review is to provide candid and critical comments that will assist the institution in making its published report as sound as possible and to ensure that the report meets institutional standards of objectivity, evidence, and responsiveness to the study charge. The review comments and draft manuscript remain confidential to protect the integrity of the deliberative process. We wish to thank the following for their review of this report:

Deane Bowers, University of Colorado, Boulder
Susan Mazer, University of California, Santa Barbara
Robert Page, Arizona State University
Peter Raven, Missouri Botanical Garden
Malcolm Sanford (retired), University of Florida
Marla Spivak, University of Minnesota
James Thomson, University of Toronto
Nickolas Waser, University of California, Riverside

Don Wilson, U.S. Fish and Wildlife Service
Ada Wossink, North Carolina State University

Although the reviewers listed above provided constructive comments and suggestions, they were not asked to endorse the conclusions or recommendations, nor did they see the final draft of the report before its release. The review of this report was overseen by Drs. Frederic L. Gould and Mary Jane Osborn. Appointed by the National Research Council, Drs. Gould and Osborn were responsible for making certain that an independent examination of this report was carried out in accordance with institutional procedures and that all review comments were carefully considered. Responsibility for the final content of this report rests entirely with the author committee and the institution.

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Summary

This report of the National Research Council's Committee on the Status of Pollinators in North America is an assessment of pollinating animals in the United States, Canada, and Mexico. To prepare this report, the committee compiled and analyzed the published literature; consulted numerous experts from academia, industry, and nongovernmental organizations; and drew from its members' extensive expertise. The extent to which the committee could discuss different pollinator species in different regions depended largely on the availability of data, as the amount and quality of evidence vary widely for different animal groups. For most North American pollinator species, long-term population data are lacking and knowledge of their basic ecology is incomplete. These information deficiencies make definitive assessments of North American pollinator status exceedingly difficult. This lack stands in contrast to the study of pollinators in Europe, where status has been the subject of systematic investigation for some time, and where declines and extinctions have been definitively documented. Notwithstanding these gaps, the committee found sufficient evidence to determine the status of a range of both managed and unmanaged pollinators in North America.

IMPORTANCE OF POLLINATORS

About three-quarters of the more than 240,000 species of the world's flowering plants rely on pollinators—insects, birds, bats, and other animals—to various degrees to carry pollen from the male to the female parts of flowers for reproduction. Pollinators are vital to agriculture because most

fruit, vegetable, seed crops and other crops that provide fiber, drugs, and fuel are pollinated by animals. Bee-pollinated forage and hay crops, such as alfalfa and clover, also are used to feed the animals that supply meat and dairy products. Animal-pollinated crops generally provide relatively higher income to growers than do crops pollinated in other ways.

Over and above its direct economic value to humans, pollination by animals provides essential maintenance of the structure and function of a wide range of natural communities in North America, and it enhances aesthetic, recreational, and cultural aspects of human activity. In view of that economic and ecological importance, this report assesses the status of pollinators in North America, identifies species for which there is evidence of decline, analyzes the putative causes of those declines, and discusses their potential consequences. The committee's statement of task is provided in Box S-1.

The first section of this summary addresses the status, causes of decline, consequences of decline, monitoring needs of managed pollinators, potential steps for managed pollinators' conservation and restoration, and the committee's recommendations (some in abbreviated form). The second section covers the same topics for wild pollinators. Detailed recommendations are provided in Chapter 7.

BOX S-1

Statement of Task:

Committee on the Status of Pollinators in North America

The National Research Council's Committee on the Status of Pollinators in North America was charged to address the following questions:

- To what degree, if any, are pollinators experiencing serious decline?
- Where decline can be established by available data, what are its causes?
- What are the potential consequences of decline in agricultural and natural ecosystems?
- What research and monitoring are needed to improve information?
- What conservation or restoration steps can be taken to prevent, slow, or reverse decline?

MANAGED POLLINATORS

Status

Findings: Long-term population trends for the honey bee, the most important managed pollinator, are demonstrably downward. Similar data are not available for other managed pollinators, such as alfalfa leafcutting bees and bumble bees.

Among the various pollinator groups, evidence for decline in North America is most compelling for the honey bee, *Apis mellifera*. Honey bees enable the production of no fewer than 90 commercially grown crops, and beekeeping is a large commercial industry that leases honey bee colonies for pollination services across the continent.

Since 1947, the U.S. Department of Agriculture's (USDA's) National Agricultural Statistics Service (NASS) has tracked honey bee colonies managed by beekeepers in the United States. Statistics demonstrate declines in 1947–1972 and 1989–1996, and a recent drop in 2005. Reports from industry journals suggest higher rates of winter kill in honey bee colonies since the advent of the parasitic mite *Varroa destructor* in the 1980s, causing temporary shortages of healthy honey bee colonies (for early season almond pollination) that are not captured by the NASS data. However, putting those declines into context is complicated by the peculiarities of NASS data collection. Because its annual survey focuses on honey production and pollinating colonies are not monitored unless they also produce honey, there are limits on the extent to which those data can be extrapolated to inform population estimates. NASS methods result in undercounting because the annual survey group consists of beekeepers with five or more hives; there is no mechanism to count hobbyist beekeepers who might nevertheless contribute to the supply of honey-producing or pollinating colonies. Moreover, because surveys do not consider that some honey-producing colonies travel—they are leased in different regions of the country for different seasons—these colonies can be counted more than once.

NASS also conducts a 5-year census of agriculture survey that counts all honey bee colonies just once, but definitional differences make the data incompatible with data from the annual honey survey. Yet another complicating factor is that no surveys account for colony health or for intrayear volatility in colony numbers. (Colonies that die early in the year, when they are critically needed for pollination, can be replaced by purchasing packages of bees or splitting surviving colonies later in the year.) Finally, there is an additional complication for assessing the supply of honey bee pollinators in North America. U.S. data collection does not match what is done in Canada or Mexico. Canadian data are collected on all honey bee colonies, whether they are kept for pollination, for honey production, or both. Mexico has

only recently begun a survey program—data collection began in 1990—and its collection methods were not available to the committee.

Recommendation: Improved information gathering for the beekeeping industry is critical, and the NASS should modify its data collection methodologies. The committee specifically recommends that NASS:

- Refine its assessment of honey bee abundance, specifically by collecting data annually, eliminating double-counting, recording pollination services, and monitoring winter losses.
- Collect commercial honey bee pollination data, including crops pollinated and leasing fees, from beekeepers and from crop growers.
- Coordinate and reconcile data collection on honey bee colonies throughout North America. NASS should make its annual survey definitions compatible with its 5-year census of agriculture. The United States should work with Canada and Mexico through the North American Free Trade Agreement's Commission for Environmental Cooperation and the Trilateral Committee for Wildlife and Ecosystem Conservation and Management to adopt common methodologies.

Causes of Decline

Findings: Introduced parasites and pathogens clearly have harmed some managed pollinators, most notably honey bees.

Introduced parasites, particularly *Varroa destructor*, the varroa mite, clearly have contributed to reductions in managed and unmanaged honey bees. In early 2005, for the first time since 1922, pollinating honey bees were imported from outside North America, a change made possible by a regulatory alteration to the terms of the Honeybee Act of 1922. The imports were permitted in part because of a shortage of honey bee colonies for almond pollination in California. Bee importation, however, can carry the risk of pest and parasite introduction. There is evidence that other factors also contribute to current and potential future declines, among them antibiotic-resistant pathogens (American foulbrood); pesticide-resistant mites; and the encroachment of Africanized honey bees, particularly in the southeastern United States, a major regional source of honey bees sold or leased in the rest of the country.

Recommendation: The Animal and Plant Health Inspection Service (APHIS) should ensure that its regulations prohibit introduction of new pests and parasites along with imported bees, and Congress should extend the Honeybee Act of 1922 in principle to other managed pollinator species.

Recommendation: Through research at the Agricultural Research Service (ARS) and competitive grant programs, USDA should not only continue but also expand its efforts to:

- Encourage innovative approaches to protecting honey bee health by
 - developing sustainable pest and resistance management programs for varroa mites, including identifying additional least-toxic alternative pesticides and nonchemical cultural bee management practices.
- Improve genetic stocks of honey bees by
 - refining methods for breeding, selecting, maintaining, and improving stocks with disease and pest resistance, moderated temperament, and improved honey production;
 - refining methods for producing high-quality queen production from selected stocks including controlling mating to ensure expression of desired traits in colonies;
 - expanding current efforts in germplasm preservation, including cryopreservation;
 - developing methods for the maintenance of European stocks in areas of Africanization;
 - developing a third-party certification program to ensure the quality and effectiveness of commercial queens; and
 - identifying genetic and genomic markers as a support to breeding programs (Chapter 6).

Although honey bees are the most important managed pollinators, other managed non-*Apis* species also require attention. The development of management protocols for wild species and the management of agricultural landscapes to sustain wild pollinator populations can create alternatives to honey bees as pollinator demands rise and shortages become likely.

Recommendation: The USDA-ARS should:

- Create research entomology positions in its fruit and vegetable laboratories in geographically diverse regions of the United States to develop new non-*Apis* pollinators and establish protocols for management. These activities should augment work in the Bee Biology and Systematics Laboratory in Logan, Utah, which currently serves as a focal point for non-*Apis* research.

- Develop and implement bombiculture¹ disease management programs to prevent pathogen spillover to wild populations.
- Address pathogen problems in culturing alfalfa leafcutter bees (megachileculture) to improve pollinator efficacy and sustainability.
- Conduct research on landscape and farm management as related to pollinators, and provide guidance on pollinator-friendly management practices.

Recommendation: Private-sector funding mechanisms for honey bee health and technology transfer from government research facilities should be created and enhanced to meet pollination needs. Industry checkoff programs, for example, could add honey bee pollination services to the existing crop commodity and honey programs. This private-sector effort could complement federally funded basic research efforts and promote translational research.²

Consequences of Decline

Findings: Managed pollinator decline and rising cost of pest control could increase pollinator rental fees.

Among the most conspicuous, demonstrable consequences of changing pollinator status is the rising cost of pest control in bee husbandry that has attended mite infestations of managed populations. Honey bee rental fees rise because of increasing demand attributable to growth in almond production and because of seasonal instability in honey bee populations. Notwithstanding, alternative managed pollinator species are not being widely utilized. And despite evidence of their efficacy as crop pollinators, wild species are not being effectively utilized.

Monitoring

Findings: As noted, improved information gathering for the beekeeping industry is critical, and the NASS should modify its data collection methodologies. In addition, the potential for the development of new management protocols to increase the use of wild pollinator species for agriculture should be explored to create alternatives to honey bees as commercial pollinator demands rise and shortages become likely.

¹Domestication of bumble bees for commercial propagation.

²Translational research is the process of applying ideas, insights, and discoveries generated through basic scientific inquiry to industrial, agricultural, and medical uses.

Recommendation: USDA should establish discovery surveys for crop pollinators throughout the range of crops in North America to identify the contributions of wild species to agricultural pollination.

Conservation and Restoration

Findings: Research in genetics and genomics has facilitated the development and maintenance of mite- and pathogen-resistant stocks of honey bees. However, these technologies have not been widely adopted, and there is a pressing need for translational research to synthesize commercially viable practices from the results of basic research.

As noted, USDA's intramural research and competitive grant programs should expand efforts to use state-of-the-art scientific knowledge to encourage innovative and commercially viable approaches to protecting honey bee health.

WILD POLLINATORS

Status

Findings: There is evidence of decline in the abundance of some pollinators, but the strength of this evidence varies among taxa. Long-term population trends for several wild bee species (notably bumble bees) and some butterflies, bats, and hummingbirds are demonstrably downward. For most pollinator species, however, the paucity of long-term population data and the incomplete knowledge of even basic taxonomy and ecology make definitive assessment of status exceedingly difficult.

Most other insect pollinators in natural and agricultural systems are not well characterized, taxonomically or ecologically, in part because of the lack of monitoring programs and in part because of a shortage of taxonomists. Overall, the paucity of long-term data prevents the documentation of population trends for almost all pollinator species. Although suggestive evidence of decline, extirpation, or extinction exists for some species, documentation of population changes is available for very few.

Notwithstanding the deficiencies in the data, there is clear evidence of decline in the numbers of some vertebrate and invertebrate pollinators. In parts of their ranges, the declines of several vertebrate pollinator species, particularly bats, are evidenced by conservation program monitoring. Long-term studies by individual investigators and regional Heritage Programs also provide evidence for declines—local and global—among wild bumble bee species and in some butterflies. Some pollinator species have been added to endangered species lists.

Recommendation: To address the taxonomic impediment to assessing pollinator status, USDA-ARS should expand basic research on the systematics of pollinators and on the development of rapid identification tools.

Causes of Decline

Findings: The causes of decline among wild pollinators vary by species but are generally difficult to assign definitively. Pathogens that have spilled over from commercially produced bumble bees for greenhouse pollination appear to have contributed to declines in some native bumble bees. Other factors for which there is convincing evidence include habitat degradation and loss, particularly for some bats, bees, and butterflies.

Definitive causes of decline or factors that contribute to decline in species with demonstrable changes in population status could be assigned in only a few cases. A major cause of decline in native bumble bees appears to be recently introduced nonnative protozoan parasites, including *Nosema bombi* and *Crithidia bombi*, probably from commercial bumble bees imported from Europe for greenhouse pollination. The bees frequently harbor pathogens and their escape from greenhouses can lead to infections in native species. Disease, notably chalkbrood (caused by the fungal pathogen *Ascosphaera aggregata*), also has harmed populations of *Megachile rotundata*, the alfalfa leafcutter bee, in the United States. In some species, competition with exotic pollinators (including *Apis mellifera*) has led to population declines.

Declines in many pollinator groups are associated with habitat loss, fragmentation, and deterioration, although in the United States data are, in most cases, inadequate to demonstrate causation unambiguously. One exception is the decline in bat populations that is attributed to the destruction of cave roosts.

There is evidence that other factors contribute to the documented declines among other pollinators. Changes in phenological synchrony and in distributions of pollinators and plants resulting from global climate change could lead to a decline in interactions between flowers and pollinators. Disruption of migratory routes is evident in hummingbirds, nectar-feeding bats, and some butterflies.

Recommendation: To prevent pathogen spillover to wild populations, APHIS should require that any commercially produced bumble bee colony shipped within the United States be certified as disease-free.

Consequences of Decline

Findings: The consequences of pollinator decline in nonagricultural systems are more difficult to define, but one important result could be an increased vulnerability of some plant species to extinction.

Few plant species rely on a single pollinator. Pollen limitation of seed set is common in wild plants, but its population consequences are not clear. In the event of declining pollinator populations, some plant populations that are dependent on affected pollinators for reproduction could become more vulnerable to an extinction vortex—the interacting demographic and genetic factors that progressively reduce small populations. Therefore, the effects of pollinator decline on rare plant species or on those with small populations also should be given special attention.

Recommendation: The U.S. Geological Survey, the Fish and Wildlife Service, and other agencies responsible for natural resource protection should establish discovery surveys for pollinators of rare, threatened, and endangered plant species.

Monitoring

Findings: Long-term, systematic monitoring is necessary for unambiguous documentation of trends in species abundance and richness. Such monitoring allows detection of relationships between changes in pollinator communities and the putative causes of change. Those relationships must be understood to assist in developing plans to mitigate harm or to manage species sustainably.

Pollinator-monitoring programs in Europe (for example, the Survey of Wild Bees in Belgium and France and the European Union's Assessing Large-Scale Risks for Biodiversity with Tested Methods project) have effectively documented declines in pollinator abundance, but there is no comparable U.S. program. The lack of historical baselines to compare with contemporary survey data makes it difficult to assess pollinator status or to determine the causes of documented declines.

Recommendation: The federal government should establish a network of long-term pollinator-monitoring projects that use standardized protocols and joint data-gathering interpretation in collaboration with Canada and Mexico. A rapid, one-time assessment of the current status of wild pollinators in North America to establish a baseline for long-term monitoring is a laudable initial goal.

Components of this two-part assessment and monitoring program should include re-surveys of areas well sampled in the past and mining of museum collections and the literature for historical data that correspond to areas of continuous, high-intensity sampling. The assessment should also include monitoring of pollinator status and function that integrates the work of professional scientists and citizen-scientists to maximize the depth and breadth of effort.

The selection of study species should correspond to the strength of evidence for decline. In view of collective evidence of population declines and possible extinctions, bees provide a logical initial focus. Lepidoptera constitute another group for which a compelling need for monitoring exists, given recent extinctions and the classifications of some species as endangered or threatened.

Conservation and Restoration

Findings: Effective conservation or restoration of pollinator populations requires comprehensive knowledge of their biology, which is currently insufficient to inform the design of sustainable management and maintenance programs. However, many simple and relatively inexpensive practices for pollinator conservation are available. Land managers and landowners, including farmers and homeowners, should be encouraged to adopt “pollinator-friendly” practices, many of which incur little expense. However, widespread adoption of these practices is unlikely unless there is a general appreciation of the ecological and economic benefits of pollinators. Hence, public outreach is key to pollinator protection, conservation, and restoration.

Recommendation: Because of the importance of pollination as an ecosystem service in both agricultural and natural ecosystems, the National Science Foundation and USDA should recognize pollination as a cross-cutting theme in their competitive grant programs. Representative areas where research is needed include identification of causes and consequences of pollinator decline, ecology, restoration, conservation, and management of pollinators and pollination services, and establishment of Small Business Innovation Research programs to promote technology transfer to address the health and sustainability of commercially managed pollinators.

Notwithstanding deficiencies in understanding of wild-pollinator biology, viable, pollinator-friendly land management practices (such as planting native plants to enhance pollinator habitat) are known and available, although not yet widely adopted. Farmers and ranchers can be offered economic incentives to adopt such practices.

Recommendation: Economic incentives should be expanded for pollinator conservation.

- State-level Natural Resources Conservation Service (NRCS) offices should provide lists of scientifically tested and approved pollinator-friendly practices to farmers participating in USDA cost share programs (the Wildlife Habitat Incentives Program and the Environmental Quality Incentives Program), land retirement programs (the Conservation Reserve Program [CRP] and the Conservation Reserve Enhancement Program), and production stewardship programs (the Conservation Security Program).
- CRP should explicitly incorporate pollinator habitat in the environmental-benefits index used to evaluate land parcel proposals and incorporate the value of pollinator habitat development into its determination of the stewardship tiers for federal payments.
- USDA cost-sharing, land retirement, and production stewardship programs should be available to producers of all commodities—fruits, nuts, and vegetables—that depend on pollinators.
- The NRCS should target new hiring of personnel whose expertise is in biological sciences, especially ecology and natural-area management.

Landowners other than farmers and ranchers—such as homeowners and businesses—also could contribute to the conservation of pollinators by planting wildflowers to provide floral resources for resident and migratory adult pollinators and by providing nesting sites for females. People who do not own or manage land also can help by participating in monitoring programs. Critical to the success of citizen-scientist programs, however, is effective public outreach to raise awareness of pollinators' ecological and economic contributions and to encourage public participation in conservation.

Recommendation: As part of their outreach, federal granting agencies should make an effort to enhance pollinator awareness in the broader community through citizen-scientist monitoring programs, teacher education, and K–12 and general public education efforts that center on pollination.

Recommendation: Professional societies (Ecological Society of America, Entomological Society of America, American Association of Professional Apiculturists, Botanical Society of America) and nongovernmental organizations (North American Pollinator Protection Campaign, Xerces Society for Invertebrate Conservation) should collaborate with landowners and the public to increase awareness of the importance of pollinators and to publicize simple activities the public can do to promote and sustain pollinator abundance and diversity.

Although the object of the Endangered Species Act of 1973 (ESA) is to protect endangered species and their habitats, many endangered pollinators are not recognized as candidate species for two reasons. First, Congress directed that listing of species requires a scientific determination of a species' continued existence as threatened or endangered, but data on many pollinators are sketchy. Second, a 1981 congressional revision of the ESA specifically exempted any "species of the Class Insecta determined by the Secretary to constitute a pest whose protection under the provisions of this Act would present an overwhelming and overriding risk to man." Some caterpillars and carpenter bees, for example, can cause economic damage. Thus, it might be difficult to present sufficient evidence to list them.

Recommendation: Congress should not consider any ESA amendment that would create additional barriers to listing pollinator species as endangered.

1

Role and Importance of Pollinators

The angiosperms—flowering plants that produce seeds often enclosed within an edible fruit—are among the planet’s most successful life forms. More than 250,000 species of flowering plants have been described, and an equivalent number could await discovery (Davies et al., 2004). At the base of most terrestrial and many aquatic food webs, the angiosperms are the principal providers of nutrients and resources to most other organisms, and they provide multidimensional structure for the majority of terrestrial and freshwater ecosystems. Humans derive food, fiber, drugs, and fuel, either directly or indirectly from angiosperms. Moreover, angiosperms have enhanced aesthetic, recreational, and cultural pursuits since before recorded history.

Reproductive systems of angiosperms vary greatly among species (Box 1-1), but two processes are necessary for sexual reproduction in all angiosperms: pollination—the transfer of pollen from the anthers of a stamen to the stigma of a pistil—and fertilization—the fusion of the sperm nuclei from pollen with the egg nucleus in the ovary to produce an embryo. Some plants self-pollinate, that is, pollen transfer occurs within the same flower or among the flowers on a single plant, usually because the anthers touch the adjacent stigma. The majority of flowering plants, however, depend on the transfer of pollen from other individuals (cross-pollination).

Although some species rely on abiotic forces, including wind and water, for pollen transfer, more than three-fourths of the planet’s angiosperms rely on over 200,000 species of animal pollinators to various extents to meet their reproductive needs. Fossil records show that angiosperms underwent a remarkable diversification between 130 million and 90 million years ago

BOX 1-1
Barriers to Self-Fertilization

Flowers can be staminate (bearing only male reproductive organs), pistillate (bearing only female reproductive organs), or perfect (bearing male and female reproductive organs). Individual plants can be monoecious (bearing staminate and pistillate flowers), dioecious (staminate and pistillate flowers borne on separate plants), or even trioecious (staminate, pistillate, and perfect flowers borne on separate plants). Within dioecy, various conditions can be found in different species; *gynodioecy*, for example, is the term applied to the breeding system of species in which individuals bear either female or hermaphrodite flowers (Richards, 1997). Almost three-quarters of all plant species produce perfect flowers. Approximately 5 percent are dioecious, and slightly more than 5 percent are monoecious (Molnar, 2004).

Pollination can occur within the flowers of a single plant, among different flowers of a single plant, and among flowers of different plants. A plant that is self-fertile and self-pollinating is called *autogamous* if pollination and fertilization take place within the same flower. A plant is *geitonogamous* if pollination and fertilization take place between flowers of the same plant, whereas a plant that is cross-pollinated and cross-fertilized is *xenogamous*. It is common for plants to receive mixtures of self and outcross (nonself) pollen grains, especially if the male and female parts are in the same flower (Plate 1—a perfect or hermaphrodite flower).

Perpetual self-fertilization could be problematic for plants because of the many potential genetic complications associated with inbreeding (Charlesworth and Charlesworth, 1987). Accordingly, adaptations that reduce the likelihood of selfing exist in many taxa. Dioecy and monoecy promote outcrossing,

and that they achieved ecological dominance 100 million to 70 million years ago (Davies et al., 2004). Chief among the many explanations offered for their spectacular ascendancy is the development of mutualistic associations with animals for the dispersal of pollen (Baker and Hurd, 1968; Faegri and van der Pijl, 1979; Labandeira et al., 1994; Stebbins, 1950, 1974) and seeds (Herrera, 1989; Kevan, 1984; van der Pijl, 1982). Mutualistic associations with animals provide mobility of gametes to otherwise predominantly sessile terrestrial plants, which allows for greater genetic variation in plants as well as access to a wider range of ecological opportunities through seed dispersal. For flowering plants, use of an animal partner to transport pollen increases the area in which potential mates can be found and promotes outcrossing, the merger of gametes from genetically distinct individuals. Increasing genetic variability through recombination associated with outcrossing is key

although monoecious plants can receive self-pollen from male flowers on the same plant. Many monoecious species produce male and female flowers at different times, and the probability of selfing is reduced. Similarly, in plants with hermaphrodite flowers, self-pollination within flowers is avoided when the male and female floral parts mature at different times. In some species, the chance of self-pollination is reduced because the male and female parts of the same flowers are separated. In a subset of those species, the male and female parts of the flower move closer together as the flower ages, allowing self-pollination as a “last resort” before the flower is too old to set fruit.

As a further deterrent to selfing, many flowering plant species are self-incompatible—that is, pollen that is deposited on a stigma within the same flower (or another flower on the same plant) is unable to achieve fertilization. Self-incompatibility is controlled in complex and variable ways, and it involves the interplay of incompatibility alleles (of which there may be many) and their effects in the two parent plants (Matton et al., 1994). The effectiveness of self-incompatibility mechanisms ranges from absolute to weak, and the mechanisms for blocking self-fertilization can break down as a result of aging or external factors, especially heat.

Breaking those barriers down ensures sexual reproduction (seed set and fruit set) even when cross-pollination is not possible. It is important to note, however, that despite the ubiquity of outbreeding, many species persist exclusively and successfully with self-pollinating and self-fertile flowers. Moreover, some self-fertile plants that can self-pollinate (including some legumes) are of agricultural importance. They can establish themselves in nonindigenous areas where their natural pollinators are absent. The nature and evolutionary biology of plant-breeding systems are presented in detail by Richards (1997).

to allowing organisms to adapt to spatially and temporally variable environments (Box 1-1). Genetic variability in plant populations could help to facilitate the evolution of resistance to pathogens and herbivores.

After fertilization is complete, the production of fruit ensues. A flower’s ovary may contain a single ovule and produce a fruit that bears only a single seed (as in the almond, avocado, coconut, plum, or cherry), or it may contain hundreds of ovules and produce a fruit bearing hundreds of seeds (as in the tomato, kiwi fruit, cucumber, watermelon, or squash). Because each seed results from the union of a sperm cell from a pollen grain and an egg cell, some plants require many hundreds of pollen grains to fertilize all of the available egg cells. If a flower receives an inadequate number of pollen grains, some of the egg cells will not be fertilized and accordingly seeds will not develop. Economic consequences of such incomplete fertilization include

production of undersized or misshapen fruit that, for a market crop, has less value. Adequate pollination often requires that individual flowers be visited by many pollinators or that one to several pollinators make multiple trips to the same flower.

Some fruits of economic importance are seedless by design. They are generally the product of selective breeding or genetic manipulation that would not be sustainable in nature (Schery, 1972). Seedless bananas, for example, are the products of sterile triploid plants arising either spontaneously or as a result of hybridization of diploid and tetraploid individuals and are propagated vegetatively. Parthenocarpic fruits, such as clementines (seedless tangerines), are those in which fruits develop in the absence of successful fertilization; fertilization could fail because these self-incompatible cultivars are grown in monoculture orchards. Seedless grapes, in contrast, are stenospermocarpic; fertilization takes place, but the resulting fruit is seedless because the immature embryo fails to develop (Schery, 1972).

POLLINATORS IN NATURAL AND AGRICULTURAL ECOSYSTEMS

In view of the fact that pollinator-plant interactions encompass almost 400,000 species, the precise nature of the relationship between plant and pollinator varies enormously. Although some animals visit flowers for nectar or pollen, not all flower visitors bring about pollination. Effective pollinators often have behavioral and anatomical traits that greatly increase the efficiency and accuracy of pollen delivery (Barth, 1991; Faegri and van der Pijl, 1979; Proctor et al., 1996). In general, pollination is a mutually beneficial interaction; pollinating animals receive some form of nutritional “reward” for visitation and pollen delivery. Pollen itself can be a reward, serving as the primary food resource for most larval bees and as an important source of protein for some flies, butterflies, birds, and bats (Roulston and Cane, 2000). Other plants provide nectar, oils, resins, fragrances, pheromone precursors, and other resources to induce visitation and pollen delivery (Barth, 1991; Buchmann, 1987; Dafni et al., 2005; Roulston and Cane, 2000; Roulston et al., 2000).

Plants and pollinators vary in their degree of interdependence. Some plant species depend primarily on a single species or genus of pollinator, which in turn has restricted sources of pollen or nectar. An example of a closely dependent association is the relationship between plants in the genus *Yucca* (Agavaceae) and their pollinators, the aptly named yucca moths of the genus *Tegeticula* (reviewed in Pellmyr, 2003). In this mutualism, estimated to be more than 40 million years old, the adult yucca moth is the primary pollinator of yucca and the developing yucca seeds the main nutritive source for the caterpillar. The female moths have unique structures, called tentacles,

which are used to collect and compact comparatively large quantities of pollen (up to 10 percent of the moth's weight) from yucca flowers. After gathering a pollen mass, the moth flies off and visits another flower, in which she lays eggs. Then, in a distinctive series of stereotyped behaviors, she places part of the pollen load directly on the stigma surface to achieve pollination and subsequent fertilization, thereby guaranteeing a food source for her offspring.

Such specialized relationships, however, are the exception in plant-pollinator interactions. In many cases, if not most, associations are highly opportunistic. Over a 2-year period, for example, at least 45 species of insects in 5 orders were observed to visit *Geranium thunbergii* flowers in a natural population; of these, 11 species in 3 orders served as principal pollinators (Kandori, 2002). Principal pollinators of a particular species can vary spatially as well as temporally; the alpine sky pilot, *Polemonium viscosum*, is pollinated primarily by bumble bees at high elevations and by flies at low elevations in its native Rocky Mountain range (Galen et al., 1987). Humans have understood the agricultural importance of pollination—that plants require pollen transfer to produce fruits and set seed—for at least 3,500 years. However, the idea that seeds result ultimately from the deposition of pollen grains on stigmatic surfaces was not clearly articulated until the 17th century (Camerarius, 1694) and even then was slow to gain acceptance. The systematist Carolus Linnaeus, for example, identified the sexual organs of plants as important components of his classification system, to the disapprobation of the 18th century's religious establishment.

The idea that animals play a role in cross-pollination, the transfer of pollen from one individual to another, was not clearly articulated until close to a century later (Kölreuter, 1761; Sprengel, 1793). Joseph Gottlieb Kölreuter, a professor of natural history at the University of Karlsruhe, Germany, demonstrated that insect visitation was a prerequisite for seed production in several economically important fruits, vegetables, and ornamental flowers and put his knowledge to practical use by developing technique for artificial fertilization and conducting the first cross-hybridization of two plant species (Mayr, 1986; Sinnott, 1946).

The great insights and practical achievements of Kölreuter and Sprengel failed for the most part to inspire their contemporaries, but a half-century later their work had a profound influence on the thinking of another biologist—Charles Darwin. The publication of *The Origin of Species by Means of Natural Selection or The Preservation of Favoured Races in the Struggle for Life* (*The Origin of Species*, in short) in 1859 ushered in a new era of experimental pollination biology. In his preface, Darwin described the process of coadaptation, which is what allows living organisms to serve as selective agents in the same manner as abiotic forces and specifically mentioned pollination as an example.

Darwin's extensive writings on plant-pollinator relationships, not only in *The Origin of Species* but also in *The Various Contrivances by which British and Foreign Orchids are Fertilised by Insects and the Good Effects of Intercrossing* in 1862 and other subsequent publications, summarized an extensive literature and described his own meticulous experiments, thereby providing compelling evidence of the significance of pollination in the lives of plants. Demonstration of the evolutionary mechanism to account for the reciprocally adaptive relationship between plants and their pollinators provided the impetus for an explosion of interest in pollination biology (Delpino, 1868–1875; Knuth, 1906, 1908, 1912; Müller, 1869; Müller and Delpino, 1869) that laid the foundation for agricultural applications and for contemporary experimental studies.

POPULATION MANAGEMENT

Active Management

Recognition of the mechanisms of biotic pollination led to important agricultural innovation, with extensive economic consequences (Box 1-2); management of pollinator species allowed for enhanced crop productivity and for commercialization (and export) of numerous crop plants. In North America, only a handful of pollinator species are actively managed—that is, they are semidomesticated, produced in large quantities, and bought and sold commercially. Of these, *Apis mellifera* L., the western honey bee, is the premier actively managed pollinator worldwide, highly valued for its activity as a pollinator and for its production of wax and honey (Delaplane and Mayer, 2000; Free, 1993; Kearns et al., 1998; McGregor, 1976).

Native to Eurasia, the honey bee has been hunted for its honey and wax for at least 6,000 years (Crane, 1983, 1990) and records of semidomestication and hive management date back to ancient Egypt (Crane, 1999). *A. mellifera* rapidly became the primary pollinator for modern agriculture, and managed colonies were transported around the world, first arriving in North America with European colonists in the 1600s (Sheppard, 1989a). Modern apiculture in North America dates to 1862, when L. L. Langstroth, a Philadelphia minister who kept bees as a hobby, exploited the concept of “bee space” to construct movable-frame, top-bar hives that allowed beekeepers to harvest honey, manipulate their colonies, and increase efficiency without harming the bees (Langstroth, 1862). Langstroth's invention resulted in the large-scale commercial beekeeping and honey industry that exists today.

Honey bees pollinate more than 100 commercially grown crops in North America (Delaplane and Mayer, 2000; Free, 1993; Kearns et al., 1998; McGregor, 1976). In the United States, about 135,000 beekeepers

manage 2.4 million colonies of honey bees. Most beekeepers (about 94 percent) are hobbyists with 25 colonies or fewer. Another 5 percent are called sideliners, each managing 25–300 colonies. Only about 1 percent are commercial beekeepers and they generally manage between 300 and 60,000 colonies each to provide most of the nation's pollination services (D. Weaver, The American Beekeeping Federation, presentation to the committee on October 19, 2005).

Beekeepers in the United States have formed hundreds of local associations and two national trade organizations. The American Beekeeping Federation (ABF) has about 1200 members (ABF, 2005), and the American Honey Producers Association (AHPA) has about 500 members (S. Park, AHPA, personal communication, June 12, 2006). The Eastern Apicultural Society, Heartland Apicultural Association, and the Western Apicultural Society meet annually and provide extensive educational opportunities for beekeepers. Many beekeepers, however, do not belong to any formal organization.

Other species of pollinators for which active management systems have been developed include several species of bumble bees (*Bombus*), mainly for pollination of greenhouse tomatoes (de Ruijter, 1997; Hughes, 1996; Kevan, et al., 1991; Macfarlane et al., 1994; Plowright, 1996; van Heemert et al., 1990), and leafcutting bees (*Megachile rotundata*) (Bohart, 1972a; Frank, 2003), which pollinate most of the alfalfa in parts of the arid Pacific Northwest (R. Bitner, presentation to the committee, January 14, 2006). To a lesser extent, alkali bees (*Nomia melanderi*) (Bohart, 1972a) also are managed for alfalfa pollination (Stephen, 2003).

Mason bees, including the Japanese horn-faced bee, *Osmia cornifrons*, are managed to some extent, mainly for pollination of apple orchards in the eastern United States (Batra, 1982; Bohart, 1972b), although they are used extensively in Japan for pollinating the entire apple crop. Several native *Osmia* species, notably *O. lignaria*, are used to pollinate apples in the northwestern United States (Bosch and Kemp, 2002) and in eastern Canada (Sheffield, 2006) and to pollinate cherries (Bosch and Kemp, 1999, 2000, 2001). Methods for cultivating this species are well developed (Griffin, 1993; Torchio, 2003).

Literature on the culture and management of many alternative pollinators is available (Batra, 1994a,b; Bosch and Kemp, 2001; Free, 1970; Kevan et al., 1990; Shepherd et al., 2003; Torchio, 1990, 2003). For some crops, bumble bees, megachilids, and other native bees are more efficient pollinators than are honey bees (Cane, 2002; Javorek et al., 2002; Maeta and Kitamura, 1981; Tepedino, 1997) and *Osmia* species serve as alternative pollinators for almonds (Bosch and Kemp, 2000; Torchio, 2003), red raspberries and blackberries (Cane, 2005), pears (Maeta et al., 1993), blueberries (MacKenzie et al., 1997; Stubbs and Drummond, 1997a,b; Stubbs et al., 1997), and sweet clover (Richards, 2003).

BOX 1-2
What Is Pollination Worth?

Pollination has value in two very different senses. Its *intrinsic value* or essential worth is conceptual, so it cannot be measured easily. The *economic value* of pollination is its worth for human ends, as determined through exchanges of goods or services (NRC, 2005).

The aggregate economic value of pollination services is the difference between what consumers are willing to pay (demand) and what it costs producers to provide those services (supply). Consumers' willingness to pay comes not only from direct "use" of pollination (for example, eating fruits of pollinated blossoms or enjoying the aesthetics of butterflies visiting garden flowers), but also from appreciation for the existence of pollinators and their services to future generations. Where markets do not exist (as for pollination services provided by wild pollinators), it is difficult to estimate economic value, although environmental economists have developed methods of approximation (NRC, 2005). Where markets exist (as for agricultural crop pollination), economic values can be estimated for discrete changes in supply and demand.

For the case of commercial honey bee pollination services, the consumers are the crop growers and the producers are the beekeepers. The demand curve that describes the number of honey bee colonies the growers are willing to rent at different prices for pollination is derived from what individual growers expect to earn from yield gains attributable to pollination; their demand depends on expected crop prices, expected yield gains, and the costs of available alternative means of pollination. Because growers raise different crops under different conditions, some are willing to pay more than others. An almond grower whose production is worth \$2,000 per acre will be willing to pay more than will a grower of apples for cider that is worth less than \$500 per acre. The supply curve that describes how many honey bee colonies individual beekeepers are willing to rent out depends on the beekeepers' costs of production and what they can earn from alternative uses of their bees. Beekeeping also differs in costs and earning opportunities. A beekeeper who must transport bees a long distance will have higher costs than will one who

An improved understanding of the mechanics of pollination and of its active management led to the commercialization and worldwide expansion of many crops, hitherto an impossibility. Common figs (*Ficus carica*) and Smyrna figs in California are a case in point. California, second only to Turkey in fig production, has 18,357 acres in fig production that was worth nearly \$10 million in 1998 (Farrar, 1999). *Ficus* species are primarily pollinated by agaonid fig wasps in highly species-specific associations (Bronstein, 1988; Machado et al., 2005). Fig production did not become established in

is close to an orchard that needs pollination. More details on supply and demand effects and an example relating to almond pollination are presented in Chapter 4.

Three basic methods have been used to estimate the value of commercial honey bee pollination services (Table 1-1). The first is simply to equate the value of services with the amount paid for them (Rucker et al., 2005). The approach does not capture potential consumer willingness to pay, nor does it account for beekeepers' production costs. The second approach also is the most common. This method is to estimate the value of pollination services by taking the total value (market price multiplied by quantity) of a crop and multiplying that value by a coefficient for the crop's estimated dependence on commercial pollination (Levin, 1983; Morse and Calderone, 2000; Robinson et al., 1989b). That approach captures consumer willingness to pay, but fails to subtract beekeepers' production costs. It attributes all crop value to pollination and ignores other inputs required to produce the crop. Neither of the first two methods considers that a shift in honey bee supply (for example, because of a new disease or pest) could raise crop prices and thus alter grower demand for pollination services (Kevan and Phillips, 2001). Southwick and Southwick (1992) attempted to capture that effect by estimating the price elasticities of demand for U.S. agricultural crops.

Even where markets exist and price effects are considered, it is impossible to make reliable estimates of the total value of an ecosystem service such as pollination. The market value of pollination supply shifts can be reliably estimated only for relatively small perturbations from values that have been observed in the past. Even the threat of a complete loss of pollination services would induce some people to pay extraordinarily high prices to prevent a total loss of the service. Others, however, would do without. Such price-quantity relationships fall well outside prior experience. For pollination services provided by wild pollinators where markets do not exist, current estimates of nonmarket value are fraught with limiting assumptions. The economic value of extreme deviations, such as losing all pollination services, cannot be soundly estimated (Heal, 2000). If calculable, the economic value of keeping pollination services would be very high, similar to their intrinsic value.

California until fig wasps were imported in the 1890s for pollination and growers learned to identify the proper species for pollination and determine overwintering requirements to synchronize wasp life cycles with the plants (McGregor, 1976; Swingle, 1908).

Although pollinators are in most cases managed for crop pollination, there are examples of pollinator management to achieve other goals. Hobby beekeepers often keep bees primarily for honey production or for personal satisfaction rather than for pollination. Honey bees have been recruited

for delivery of various biological control agents to protect field and greenhouse-grown crops against fungal pathogens and pests (Kevan et al., 2005). Bees are used to deliver *Bacillus subtilis* to blueberry flowers to suppress *Monilinia vaccinicorymbosi*, or mummy berry disease, a devastating fungus (Dedej et al., 2004). They also have been used to deliver *Trichoderma harzianum* 1295-22, a commercially produced agent for control of the pathogenic fungus *Botrytis cinerea* on strawberries (Kovach et al., 2000). There is a continuing effort to investigate the potential of honey bees as biological monitors for environmental contaminants (Bromenshenk et al., 1995) and land mines (Bromenshenk et al., 2003).

Passive Management

In addition to active management, pollinators can also be managed passively—that is, their activities can be manipulated by altering environmental conditions to promote their diversity and population growth or to influence particular behavior (Shepherd et al., 2003; Vaughn et al., 2004). Passive management includes farming to promote the growth of floral resources, providing artificial nest materials and nest sites, and protecting nesting habitat. All of these practices are designed to increase the diversity of the pollinator community and the abundances of particular species (Kevan et al., 1990; Kremen and Chaplin, in press).

VALUE OF POLLINATION

Pollination as a biotic process has both commercial and ecological value. In the context of agriculture, pollination provides a wide range of benefits to a broad diversity of commodities across North America. In some cases, production of the commodity itself results directly from the act of pollination (for example, fruit production). In other cases, although pollination does not result in production of the commodity itself, the process contributes to crop propagation (for example, production of seeds used to grow a root crop such as carrots) or quality (for example, size of tomatoes has been linked to repeated pollination). There are indirect benefits as well, through food-chain relationships. Alfalfa seed, a bee-pollinated crop with an annual value of \$109 million (direct effect), is used to produce hay for livestock forage that is valued at \$4.6 billion per year (indirect effect) (Morse and Calderone, 2000). Although these indirect effects tend to exaggerate the economic value of pollination, they have been used in several widely cited studies (see Table 1-1).

The annual value of honey bee pollination to U.S. agriculture has been variously estimated at \$150 million (Rucker et al., 2005), \$1.6–5.7 billion (Southwick and Southwick, 1992), \$9 billion (Robinson et al., 1989a),

TABLE 1-1 Value of U.S. Agricultural Production Attributable to Honey Bee Pollination: Comparison of Studies

Study	Reference Year	Total Value (\$ billion)	Direct Crop Value (\$ billion)	Indirect Crop Value ^a (\$ billion)	Animal Value (\$ billion)	Notes
Levin, 1983	1980	19.0	5.9	6.0	7.2	Author attributes 10% of cattle value to bees via alfalfa hay
Robinson et al., 1989 ^{a,b}	1985	9.7	6.1	3.6	0	
Southwick and Southwick, 1992 ^b	1986	5.7	5.7	0	0	Value based on price elasticity of supply change
Morse and Calderone, 2000	1996–1998	14.6	7.8	6.7	0	
Rucker et al., 2005	2004	0.15	0.15	0	0	Value is pollination fees paid

^aCrops that receive indirect benefits include alfalfa hay, asparagus, broccoli, carrot, cauliflower, celery, onion, and sugar beet.

^bEstimate for no replacement of bees; no price effects.

\$14.6 billion (Morse and Calderone, 2000), and \$18.9 billion (Levin, 1983). The annual benefit of honey bee pollination in Canada has been estimated at \$443 million by Scott-Dupree and colleagues (1995). More recent data are shown on the website of the Canadian Honey Council (<http://www.honeycouncil.ca/users/folder.asp>). The lowest U.S. figure is an estimate of the annual value of pollination fees actually paid by farmers (Rucker et al., 2005)—a value that does not capture the higher fees that farmers would be willing to pay to ensure good pollination. Table 1-1 compares studies that include estimates of such willingness to pay for pollination services and it provides a breakdown of total reported values as direct benefits to crops, indirect benefits to crops, and indirect benefits to livestock. The value of direct benefits to crops clusters in the range of \$5 billion to \$10 billion (the higher end adjusted to 2005 dollars). Values reported by Morse and Calderone (2000) and by Levin (1983) include indirect benefits of the honey bee pollination required for seed production in alfalfa hay, asparagus, broccoli, carrot, cauliflower, celery, onion, and sugar beet. Levin (1983) included 10

percent of the value of cattle and dairy production that he attributed to alfalfa hay whose seed requires bee pollination. Attributing the full market value of such indirect effects to pollination exaggerates the economic value of pollination services, because indirect products like alfalfa hay or cattle require many production inputs besides alfalfa seed. Even the alfalfa seed made possible by pollination requires that farmers provide other costly production inputs. These and other limitations of estimating economic values are discussed in Box 1-2. Given the estimates currently available, consistent comparisons can be made across those economic values based on the direct effects of pollinators.

The contributions of *A. mellifera* are not unique: Alfalfa leafcutting bees and bumble bees also pollinate crops. An estimated \$2 billion to \$3 billion value in annual crop pollination can be attributed to the activities of native bees and other insects (Losey and Vaughn, 2006; Prescott-Allen and Prescott-Allen, 1986; Southwick and Southwick, 1992).

Some vertebrates also operate as pollinators of ecologically and economically important plants. Tropical trees of the family Bombacaceae, which includes species used for timber, silk cotton, balsa wood, and other products, rely primarily on bats for pollination (Bawa, 1990; Watson and Dallwitz, 1992). Many columnar cacti and agaves, which are important sources of alcoholic beverages (tequila, mescal) and other products (sisal fibers), also depend on bats and birds for pollination (Arizaga and Ezcurra, 2002; Arizaga et al., 2002; Fleming et al., 2001a,b; Grant and Grant, 1979; Rocha et al., 2005; Valiente-Banuet et al., 1996; but see also Slauson, 2000, 2001). Globally, pollinators are fundamentally important for the production of roughly 30 percent of the human diet and most fibers (cotton and flax), edible oils, alcoholic beverages, nutraceuticals, and medicines created from plants (Buchmann and Nabhan, 1996; McGregor, 1976; Roubik, 1995).

Estimating the value of pollinators and pollination in natural ecosystems and predicting the consequences of their losses are considerably more challenging than estimating their economic value in agriculture. Such estimates are complicated by both the number of species involved (globally, more than 400,000) and the relative paucity of information available for most of those species. For example, in their effort to calculate the economic value of ecological services provided by insects, Losey and Vaughan (2006) did not attempt to place a dollar value on the contributions of pollinators to maintenance of natural plant communities, although it is reasonable to assume that a significant proportion of plants in uncultivated terrestrial communities rely upon pollinators. These plants, in turn, contribute to many ecosystem services of value to humans, such as water filtration, carbon sequestration, and flood and erosion control (Daily et al., 1997). An added complication is that insect pollinators may contribute ecosystem services other than pollination in their larval stages. The value of these services is

equally difficult to calculate, particularly without a complete understanding of all aspects of pollinators' life histories.

Dobson et al. (2006), however, developed a system for assessing the susceptibility of different ecosystem services to species loss. According to this system, which takes into consideration trophic level interactions, redundancies, and competition, ecosystem services are classified into Types A through E, with Type A services at one extreme identified as those in which species losses are mostly compensated for by co-occurring species and Type E services identified as "the most brittle services; for these services, small changes in species biodiversity result in large changes in the provisioning of ecosystem services." In Type C, an intermediate response, a linear decline in ecosystem service is expected with each species loss. In this system, pollination is considered a Type C or E service for most ecosystems, with species losses having significant impacts on trophic stability. Indeed, pollination is the only mutualistic association singled out by Dobson et al. (2006) for assessment.

STATE OF KNOWLEDGE

The study of pollinator-plant interactions is a thriving, albeit small, area of inquiry. There are no professional societies dedicated to this pursuit, and publications in the field appear in a wide range of journals. A search of the Ovid serials database with the keyword "pollination" yields 6906 publications for the period 1990–2005, with the numbers steadily increasing from 2000 onward (see also Figure 1-1 in Kearns and Inouye, 1993). Although several universities alone or in partnership with state agencies offer classes on bees and beekeeping (for example, <http://www.masterbeekeeper.org/masterbeekeeper.htm>, <http://www.ento.vt.edu/~fell/apiculture/summer/summerb.htm>, <http://www.life.uiuc.edu/entomology/bee-course.html>, <http://www.news.cornell.edu/Chronicle/00/5.11.00/bee-course.html>, http://neipmc.org/ipm_news_popover.cfm?id=821), courses in pollination biology are rare, although it often is included as a topic in seminars on plant-insect interactions (University of Southern Mississippi, Auburn University, Mesa State College, University of Toronto, Canada). Classes in pollination biology have been taught in recent years at the University of Arizona, University of California (Davis and Berkeley), University of Maryland, University of Texas at Austin, St. Louis University, Humboldt State University, and California State University at Fullerton. In Canada, pollination biology courses have been recently offered at the University of Guelph, Ontario, and at the University of Manitoba. In Puerto Rico, a course is offered at the Departamento de Química y Biología (<http://mail.udlap.mx/~cvergara/EcolPol/EcolPol.html>). Many pollination biologists, conservationists, and land managers benefit from an annual 10-day class (the Bee Course, now in its ninth year, <http://>

research.amnh.org/invertzoo/beecourse) on the systematics and biology of bees native to the southwestern United States and Mexico that is presented by the American Museum of Natural History-Southwestern Research Station at Portal, Arizona. In 2006, the McGuire Center for Lepidoptera & Biodiversity in Gainesville, Florida, announced plans to offer a course on “natural history and identification, captive propagation, host plant care and needs, field/lab research techniques, permitting/recovery planning basics, population monitoring, habitat restoration, butterfly exhibitry, education and outreach, partnership building,” and the like (<http://www.aza.org/prodev/ButterflyCon/>).

Despite the widely held assumption that “the birds and the bees” in its literal sense is a concept that is familiar even to schoolchildren, incorporation of pollination biology into primary and even secondary science curricula is far from routine. There are no specific references, for example, to pollination biology or pollinators in the National Academy of Sciences’ own set of science education standards (NRC, 1996) or in the benchmarks for scientific literacy published by the American Association for the Advancement of Science (AAAS, 1994).

HISTORY OF CONCERN

Concerns about the status of pollinators in North America over the last quarter-century have arisen in two different contexts. The agricultural community has voiced concerns over fluctuations in the health and availability of *A. mellifera*, the principal managed pollinator in the United States, and associated impacts on crop production, whereas the ecological community has noted declines worldwide as part of a larger effort addressing biodiversity losses and associated impacts on ecosystem services.

Managed Pollinators

Although the U.S. Department of Agriculture’s (USDA’s) National Agricultural Statistics Service (NASS) reported that 4.2 million colonies of honey bees were managed by beekeepers in the United States in 1981, the detection of the parasitic honey bee mites *Acarapis woodi* Rennie and *Varroa destructor* (formerly *V. jacobsoni* Oud; see Anderson and Trueman, 2000) in the United States in 1984 (Anonymous, 1987; Delfinado-Baker, 1984) and in 1987 (Delfinado-Baker 1988), respectively, ushered in an era that has been marked by fluctuations in colony numbers that is overlaid by a general downward trend (Chapter 2). Although *A. woodi* was very damaging immediately after its introduction, North American honey bee populations exhibited some resistance (Chapter 3) and, after several years, deaths from that parasite appeared to decline. However, the actual contribution of this

parasite to changes in honey bee colony numbers was never clearly established. Today, the primary concern among beekeepers is the varroa mite, which continues to cause major losses of managed hives (Caron and Hubner, 2001; Finley et al., 1996; Lumkin, 2005). Infection with *V. destructor* is fatal to most honey bee colonies of European ancestry (Beetsma, 1994; DeJong, 1990; DeJong et al., 1984; Matheson, 1994; Morse and Gonçalves, 1979). The high rate of mortality is the combined result of several factors, including low levels of natural resistance to mites in the honey bee population; inadequate stock development and production facilities; widespread use of pesticides, which helps to maintain mite-susceptible genotypes in the honey bee population; and widespread pesticide resistance in the mite population.

Few honey bee breeding programs (artificial selection) have successfully consolidated low levels of existing mite resistance into strains with significant levels of mite resistance (Harbo and Harris, 1999a). Although these strains hold promise for mite management, they are slowly being integrated into beekeepers' management programs (Chapter 6; Sheppard, 2006).

Honey bees have been widely regarded as having suffered under the weight of those stresses. NASS's 2005 estimate of 2.41 million honey bee colonies in the United States is a 28 percent decline from the pre-mite 1981 numbers, after correction for a 1985 change in NASS methodology¹ (Chapter 2). Also, parasitic mites had, by all accounts, an even more serious and negative effect on the population of feral honey bee colonies (Hoopingarner, 1991; Kraus and Page, 1995; Loper, 1995, 1996, 1997).

These losses occurred as demand for agricultural pollination services was increasing dramatically, particularly for crops that depend completely on pollinators. The almond-growing business presents a compelling example (Figure 1-1). Over the 25 years between 1980 and 2005, U.S. almond acreage increased by nearly 70 percent. Approximately 1.4 million bee colonies are needed to pollinate 550,000 acres of almonds in California, and in 2005 a shortage of colonies led to imports of colonies from Australia (Flottum, 2005). According to forecasts of the California Almond Board (cited in Sumner and Boriss, 2006), almond growing will expand to 850,000 acres by 2012, eventually requiring the services of 2.12 million colonies of pollinators. Other pollinator-dependent crops include squash (Figure 1-2) and muskmelon (cantaloupe) (Figure 1-3); domestic production of these crops has nearly doubled over the past two decades.

The growth in demand for crop pollination is not restricted to field crops. Although USDA does not collect data on acreage of greenhouse tomatoes, other sources suggest a recent large increase. Total greenhouse crop

¹In 1985, NASS stopped counting beekeeping operations with fewer than five colonies. The result was an estimated reduction of 0.86 million in the number of colonies meeting its count criterion (Muth et al., 2003, p. 498).

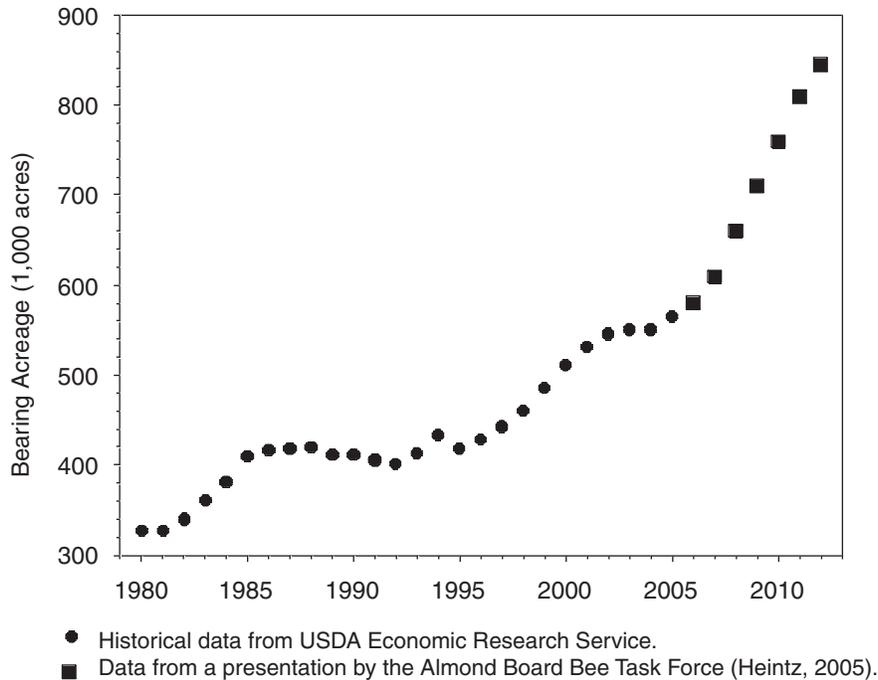


FIGURE 1-1 Bearing acreage of U.S. almond trees in 1980–2010. Almost all almonds are grown in California.

acreage increased by 40 percent between 1996 and 1999 (Dodson et al., 2002). In Mississippi, the number of commercial growers went from 15 in 1988 to about 130 in 2006 (Mississippi State University Extension Service, 2006; Snyder, 2006). The top 15 states in greenhouse tomato production had almost 600 acres in cultivation in 1999 (Snyder, 1999); in 2002, the total was about 750 acres (Dodson et al., 2002). Greenhouse tomatoes require pollination that is now accomplished mainly by managed colonies of bumble bees (Chapter 3). The growth in production suggests the demand for those bees will increase as well.

Wild Pollinators

Concerns about pollinator status are in at least one way unique in discussions of threats to biodiversity in general, in that such concerns are often directly and explicitly linked to concerns about the status of another group of organisms—the mutualistic flowering plant partners of pollinators. Over the past quarter-century, declines in wild pollinator populations

of various descriptions have been reported in Europe, Asia, Central and South America, Africa, and Australia (Allen-Wardell et al., 1998; Biesmeijer et al., 2006; Donaldson, 2002; Kearns et al., 1998; Oldroyd and Wongsiri, 2006; de Ruijter, 2002). By contrast, few pollinator species are monitored in North America. Declines in bat populations have been so dramatic that two of the three U.S. species—the lesser long-nosed bat (*Leptonycteris curasoae*) and the Mexican long-nosed bat (*L. nivalis*)—are now listed as endangered under the terms of the U.S. Endangered Species Act. All three species are listed on the federal list of species at risk of extinction in Mexico (SEMARNAT, 2002). Around the world, almost half of the insect extinctions documented have involved flower-visiting species (Appendix C). The first insect to be listed as officially endangered in the United States (Appendix D) was the Schaus swallowtail, *Papilio aristodemus*, a flower-visiting species and a presumed pollinator. Flower-visiting Lepidoptera, many of which are actual or potential pollinators, currently dominate the list of endangered species: 17 species of butterfly and 3 species of moth constitute more than half of all insect species listed as endangered (<http://ecos.fws.gov/servlet/TESSWebpage>) (Appendix D). Evidence for population decline

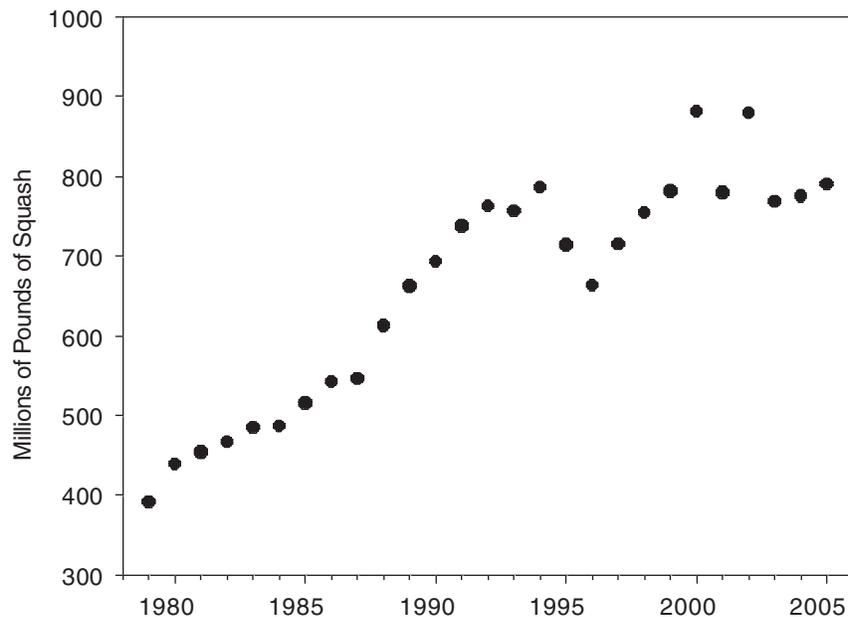


FIGURE 1-2 U.S. squash production, 1980–2005. Available evidence shows that squash plants must be pollinated by insects, and that honey bees are the chief pollinators (McGregor, 1976). Source: USDA-NASS.

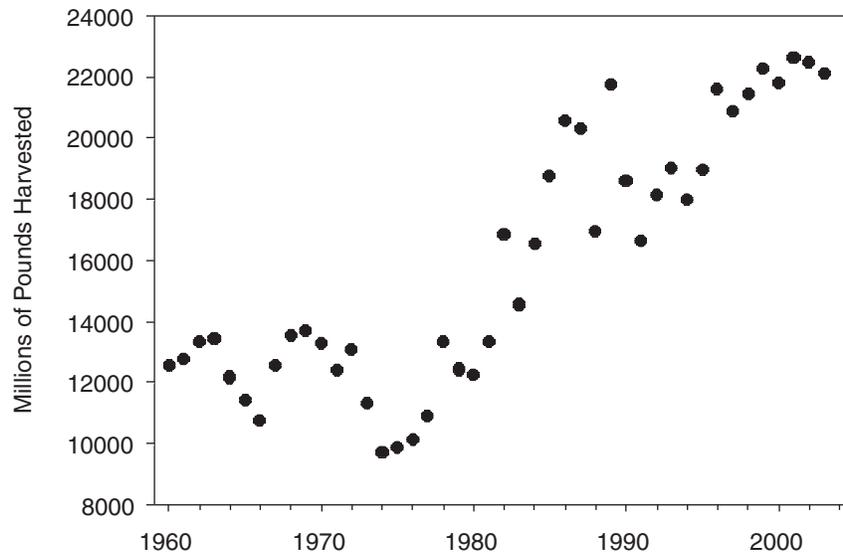


FIGURE 1-3 U.S. muskmelon production, 1960–2006. Flowers must be pollinated to produce cantaloupes. Source: USDA Economic Research Service.

(Appendix E) and local population extinction of other pollinators has begun to accumulate (Kremen et al., 2002a; Larsen et al., 2005).

Comprehensive recognition of the value of ecosystem services provided by pollinators (Daily et al., 1997; Kremen et al., 2002a, Kremen and Chaplin, in press) is relatively recent and quantitative studies on pollinator populations in North America are few in number. Among the possible causes suggested for declines in wild pollinator numbers are fragmentation, degradation and loss of habitat, nontarget effects of agricultural pesticides, competition from invasive species, and introduced diseases (Johansen, 1977; Kearns et al., 1998; Kevan, 1974, 1975a, 1999, 2001; Kremen and Ricketts, 2000; Morandin et al., 2005; Rathcke and Jules, 1993).

Efforts to Address Concern

The concept of a pollinator “crisis”—localized extinctions and possibly a global decline in the number and viability of pollinating species contributing to trophic collapse (*sensu* Dobson et al. 2006)—began to gain recognition as a critical issue in the early 1990s. Major losses in managed honey bee colonies led to concern in the United States about this critical pollinator (Watanabe, 1994). The publication of *The Forgotten Pollinators* (Buchmann and Nabhan, 1996), which extended the concern to nonmanaged species

and placed the issue within the greater context of biodiversity decline, galvanized the ecological community. Buchmann and Nabhan's book concluded with a call for a U.S. national policy on pollination and pollinators. Subsequent emphasis of pollination as a fundamental "ecosystem service" (Daily et al., 1997) led to an explosion of interest in the international policy arena (Allen-Wardell et al., 1998; Costanza et al., 1997; Eardley et al., 2006).

Among the first international efforts to address concern specifically about the status of pollinators was a proposal by the government of Brazil at the second meeting of the Subsidiary Body on Scientific, Technical and Technological Advice (SBSTTA) of the Convention on Biodiversity, which convened in Montreal, Quebec, September 2–6, 1996 (Appendix F). The purpose was to establish a program in agricultural biodiversity, which includes an "international pollinator conservation initiative" (Campanhola et al., 1998). Subsequently, the Third Conference of the Parties (COP3) to the Convention on Biodiversity (CBD), which met in Buenos Aires, Argentina, November 4–15, 1996, drafted Decision III.11, "Conservation and Sustainable Use of Agricultural Biodiversity," identifying pollinators as a "priority group" for case studies. That, in turn, led to an International Workshop on Conservation and Sustainable Use of Pollinators in Agriculture, which placed an emphasis on bees, when it met in São Paulo, Brazil, in October 1998. The workshop report, *Pollinating Bees: The Conservation Link Between Agriculture and Nature. Proceedings of the Workshop on the Conservation and Sustainable Use of Pollinators in Agriculture, with Emphasis on Bees* (Kevan and Imperatriz Fonseca, 2002), included the "São Paulo Declaration on Pollinators," which proposed the establishment of an International Pollinator Conservation Initiative (Dias et al., 1999). An early response to that call was made at the first meeting of the Systematics Society of Southern Africa, which founded the African Pollinator Initiative in January 1999.

The São Paulo proposal was ultimately presented by the Brazilian government to the SBSTTA at its fifth meeting and, at COP5—the fifth meeting of the Conference of the Parties—the International Initiative for the Conservation and Sustainable Use of Pollinators was created. That initiative was to promote international cooperation with several goals:

- Monitor pollinator decline, its causes, and its impact on pollination services.
- Address the lack of taxonomic information on pollinators.
- Assess the economic value of pollination and the economic impact of the decline of pollination services.
- Promote the conservation and the restoration and sustainable use of pollinator diversity in agriculture and related ecosystems (CBD, 2005, p. 2).

The United Nations Food and Agriculture Organization was invited to coordinate the initiative among the participating nations and agencies and to devise a plan that was based on the recommendations in the São Paulo Declaration on Pollinators. In April 2002, the International Pollinator Initiative was approved at the sixth meeting of the Conference of the Parties, which was convened in the Netherlands (www.biodiv.org/doc/meetings/sbstta/sbstta-07/official/sbstta-07-09-add1-en.doc). In March 2006, at the United Nations Convention on Biodiversity, Conference of the Parties, general meeting 8 in Curitiba, Brazil, the publication, *Pollinators and Pollination: A Resource Book for Policy and Practice* (Eardley et al., 2006), was heralded.

Between 1995 and 1999, the tri-national (United States, Canada, Mexico) Forgotten Pollinators (FP) Campaign was co-founded and directed by Gary Nabhan and Stephen Buchmann at the Arizona-Sonora Desert Museum in Tucson, Arizona. During its later years, the FP Campaign shifted its emphasis to focus on migratory pollinators (bats, hummingbirds, white-winged doves, monarch butterflies) in the United States and Mexico. In 1999, the North American Pollinator Protection Campaign (NAPPC) was launched by the Coevolution Institute in San Francisco, California, in collaboration with the National Fish and Wildlife Foundation. NAPPC is a tri-national public-private partnership of more than 100 organizations and agencies that promote pollinator awareness, policies, educational outreach, research, and conservation. Also in 1999, USDA and the U.S. Geological Survey (USGS) sponsored a joint meeting in Logan, Utah (Tepedino and Ginsberg, 2000), to explore the issue of pollinator decline. In November 1999, the USDA Agricultural Research Service (ARS) convened a workshop to obtain stakeholder input from state departments of agriculture, universities, pesticide companies, beekeepers, and extension agents on research priorities for the Bees and Pollination Component of the Crop Production National Program Writing Teams. These teams were formed at each of the workshops and consisted of ARS scientists and members of the ARS National Program Staff. The first function of each was to identify problem area topics for inclusion in the National Program Action Plan. Subsequently, individual team members were assigned as principal authors for each area identified. Writing teams and individual writers used input from the workshops, their own knowledge, and input from other ARS scientists and cooperators to identify research goals and activities to develop this action plan (http://www.ars.usda.gov/research/programs/programs.htm?np_code=305&docid=883).

Also in 1999, the National Science Foundation (NSF) funded a meeting at the National Center for Ecological Analysis and Synthesis (NCEAS) on pollinator decline, the proceedings of which were published in 2001 (<http://www.ecologyandsociety.org/vol5/iss1/art1/>) in the journal *Conserva-*

tion Ecology (now *Ecology and Society*). NSF also provided funds in fiscal years 2005–2007 for a series of NCEAS workshops to determine how to restore pollinators and pollination function in degraded landscapes. Other federal agencies with an interest in pollinator status include the U.S. Fish and Wildlife Service’s Division of Environmental Quality, which maintains a pollinator website (<http://www.fws.gov/contaminants/Issues/Pollinators.cfm>) that has statements on pollinator decline. The USGS National Biological Information Infrastructure, a collaborative program designed to provide access to data on natural resources within U.S. borders, also has a pollinator decline program (<http://www.nbio.gov>).

CHARGE TO THE COMMITTEE

In 2002, NAPPC approached the National Research Council with a request for a study to review the literature on pollinating animals in North America. With funding provided by USDA, USGS, and The National Academies, the National Research Council’s Board on Life Sciences and Board on Agriculture and Natural Resources jointly convened an ad hoc committee to document the status of pollinating animals in North America. The questions to be addressed included whether, and to what degree, pollinators are experiencing serious decline; in cases where decline can be established by available data, what its causes are; and what the potential consequences of decline might be in both agricultural and natural ecosystems. The study committee was tasked to make recommendations on research and monitoring needs to provide improved information and on any conservation or restoration steps that could prevent, slow, or reverse potential decline. The committee also was asked to compile and analyze the published literature, determine the current state of knowledge on pollinator status, identify knowledge gaps, and establish priorities for addressing these gaps.

To address its charge, the committee assessed the status of pollinators in the United States, Canada, and Mexico between the Atlantic and Pacific Oceans (Chapter 2) and some of the causes of decline in pollinator populations (Chapter 3). However, the extent to which the committee could discuss each species in different regions depended largely on the availability of data. The proportion of the report devoted to honey bees reflects the amount of knowledge and data available for this species. In contrast, the proportion of the report devoted to wild pollinators reflects the sparse data and our incomplete knowledge on those groups despite their critical role in ecosystem functioning. The later chapters of the report discuss the potential impact of pollinator decline in agriculture and natural areas (Chapter 4) and suggest ways to monitor, conserve, and restore managed and unmanaged pollinators (Chapters 5 and 6).

2

Status of Pollinators

A definitive assessment of the status of pollinator populations in North America will hinge on the quality and availability of data from a variety of well-corroborated sources, and such information is not available for every taxon. Because of their economic importance, actively managed pollinators are more likely than are wild pollinators to be closely and systematically monitored. But even when standardized data are available, interpretation of patterns of population change can be difficult. Ascertaining a pattern of decline in wild pollinator species involves consideration of a broader range of sources of information, including historical accounts, natural history collections, recently published observations, and comparative analyses. For some species, population data that are sufficient to inform an assessment of pollinator status simply do not exist.

POLLINATORS AND THE CONCEPT OF DECLINE

Identifying population declines, particularly for insects, is problematic primarily because, for many species, there are no historical data on absolute abundance. Historical accounts (for example, Jones and Kimball, 1943) often described abundance not quantitatively but qualitatively—a species might be called “common,” “uncommon,” or “rare”—so the information is difficult to interpret or compare. There are, however, numerous reports of declines of pollinating insects that have been documented according the strict criteria of federal or state law or regulations or by nongovernmental organizations. A case in point is the Massachusetts Endangered Species Act (MESA; 321 CMR 8:00), which requires demonstration of habitat

threat and population decline before an animal or plant can be listed as endangered, threatened, or of special concern—terms that themselves are suggestive of particular patterns of population change. However, different jurisdictions can define terms differently, and that causes difficulty for comparative studies of decline or endangerment. Some species also have inherently small populations and restricted ranges, and their relative rarity might not be the result of declining population.

In determining whether pollinator populations are declining, it is important to acknowledge the distinction between a “decline” and a “shortage.” An economically driven shortage of pollinators that occurs as a result of increased demand could be entirely independent of the condition of pollinator populations. In this report, the term “decline” is applied to populations for which the number of individuals is decreasing over time; “shortage” means that the supply of pollinators or their services is insufficient to meet demand. The status of pollinator populations and assemblages can be assessed in many ways, both direct and indirect (see Appendix G for examples of methods for analyzing pollinator status).

POPULATION TRENDS

Insect Pollinators

Although more than 750,000 insect species have been described (Grimaldi and Engel, 2005), possibly as many as 30 million more await discovery and formal description (Erwin, 1982; Stork, 1988, 1996; see also May, 1999, and Erwin, 2004). Insects comprise the most diverse assemblage of terrestrial animals, including within their ranks some of the most economically important pollinators and the dominant pollinators in a variety of natural systems. In some communities, insects pollinate as many as 93 percent of the flowering plants (Bawa, 1974, 1990; Kato, 2000). Unfortunately, the available taxonomic expertise does not exist to document fully the Earth’s insect biodiversity (Box 2-1); it is a virtual certainty that many insect pollinators have yet to be discovered and identified. Notwithstanding the existence of taxonomic impediments, a substantial body of information is available on pollinator population trends. The quality of this information, however, varies with taxon as, accordingly, do conclusions about the status of pollinators in these groups.

Ants, Bees, and Wasps (Order Hymenoptera)

The order Hymenoptera is a diverse and economically important group of approximately 125,000 described species comprising plant-feeding sawflies, parasitic and nonparasitic wasps, ants, and bees (Zayed and Packer,

BOX 2-1
Diversity and the “Taxonomic Impediment”

Insects account for more than half of the estimated 1,586,800 species that have been formally described by scientists (Grimaldi and Engel, 2005). The most current estimates of species undescribed or unknown to science range from 10 million to 30 million (Grimaldi and Engel, 2005; Stork, 1988, 1996); and many of the most species-rich groups are among the least thoroughly characterized. Because of a lack of available expertise, it is often impossible to identify (or “determine”) specimens.

Taxonomy and its applied interface, identification, are fundamental to continuing the study and conservation of organisms. As knowledge of living systems grows more comprehensive, the scientific community demands more from taxonomy than simply identifying which species to avoid and which are edible or otherwise useful. That the rate at which species are becoming extinct appears to exceed the rate at which new species are described (Hambler and Speight, 1996) poses not merely an academic problem but a daunting challenge to understand biodiversity with economic potential before it disappears. The problem applies to the study of plant-pollinator interactions in North America as some pollinating insects, particularly beetles and flies, are yet to be discovered and described.

The Global Taxonomic Initiative is attempting to reduce the bottleneck in taxonomic research resources in the face of what has been called the greatest extinction crisis in roughly 60 million years (J.A. Thomas et al., 2004). Under

2005). The order includes within its ranks the principal managed pollinators of the world, bees in the genera *Apis*, *Bombus*, *Megachile*, *Osmia*, and *Melipona*, as well as numerous unmanaged species of bees (Box 2-2) and wasps that represent a variety of families.

Honey Bees (*Apis mellifera*)

Nearly 17,000 species of bees have been formally described, and as many as 30,000 are estimated worldwide (Michener, 2000; T. Griswold, U.S. Department of Agriculture [USDA] Bee Biology and Systematics Laboratory, presentation to the committee, October 18, 2005). Although other species are often more efficient pollinators than are honey bees on a flower-by-flower basis, honey bees are, for many reasons, the pollinator of choice for most North American crops. *A. mellifera* is highly suitable as a commercial pollinator because of its biology (Hoopingarner and Waller, 1992;

the leadership and authority of the Convention on Biological Diversity, the initiative has two aims: (1) to increase the efficiency of biological systematics, and (2) to bolster the number of practicing, professional systematists. Critical to the development of greater understanding is a supply of professional taxonomists, usually university-trained scientists with doctorates in their disciplines.

The taxonomic impediment is far from an insoluble problem. The Consortium for the Barcode of Life is an international initiative to develop DNA barcoding as a global standard for identifying specimens. DNA barcoding uses a short gene sequence from a specific region of a genome as an identifying marker for a species (<http://barcoding.si.edu>). DNA barcoding promises to provide a rapid and inexpensive means of identifying specimens by matching barcode sequences with those of taxonomically validated vouchers. In the United States, steps to ameliorate the shortage of professionals include the highly successful program of the National Science Foundation (NSF) Partnerships for Enhancing Expertise in Taxonomy, which supports taxonomic research and training (Rodman and Cody, 2003). Assembling the Tree of Life—another NSF effort—involves advanced molecular and optical technology, readily disseminated Web-based initiatives, and increasingly advanced analytical software. Whether the federal government will continue to support and expand such programs is an open question. Hence, the first challenges to solving the taxonomic impediment in North America and globally are to assess available resources and identify the support and resources needed to reduce or eliminate taxonomic impediments.

Winston, 1987). In contrast to most other species of bees that have annual nests founded by individual, overwintered females each spring, honey bee colonies are perennial. Honey bee populations range between 10,000 and 30,000 individual worker bees, even at their nadir in late winter and early spring. Thus, honey bee colonies are able to muster large numbers of pollinators when they are needed for late winter and early spring blooms, as well as throughout the rest of the growing season. As a generalist, the honey bee can pollinate many agricultural crops, including almond and blueberry. Because it forages over long distances (up to 14 km from its nest), it is useful in expansive monocultures where wild bees of other species with more limited foraging ranges are restricted to field margins. In addition, honey bees exhibit sophisticated communication, which increases foraging efficiency, and floral constancy; individuals repeatedly visit a single plant species during each foraging trip and can recruit nestmates to flowers of that species (von Frisch, 1967). Thus, honey bees' behavior increases the

BOX 2-2

Sociality and Bee Pollination

Of the nearly 17,000 described species of bees (Michener 2000), the vast majority are solitary. Each female makes her own nest and cares for her own offspring. Among the species of pollinators that are actively managed, *Megachile rotundata*, *Nomia melanderi*, *Osmia cornifrons*, and *Osmia lignaria* all exhibit this solitary lifestyle.

The other species of bees that are actively managed for pollination in North America, *Apis mellifera* and various species of *Bombus*, are “eusocial.” Eusociality is defined by three traits: (1) cooperative care of young by members of the same colony; (2) reproductive division of labor, with more or less sterile individuals (“workers”) working on behalf of fecund colony members (“queens”); and (3) an overlap of at least two generations of adults in the same colony (Michener, 1969; Wilson, 1971).

Eusociality is the most extreme form of social organization in the animal kingdom (Wilson, 1971). It is relatively rare, limited to termites (order Isoptera), several groups of Hymenoptera (all ant species and several lineages of bees and wasps), and a few species of aphids, thrips, beetles, shrimp, and mammals (Crespi and Yanega, 1995; Sherman et al., 1995). Eusociality plays a prominent role in pollinator behavior, especially in the case of the honey bee.

Division of labor for reproduction lies at the heart of eusociality. Hymenoptera display the haplodiploid mode of sex determination; fertilized diploid eggs develop into females and unfertilized haploid eggs develop into males. Females can develop into either queens or workers. Queens specialize in reproduction, laying up to several thousand worker eggs per day. Workers engage in little if any personal reproduction, and perform all tasks related to colony maintenance and growth, including foraging.

Eusocial species are divided into two groups: primitively eusocial and advanced eusocial. In most primitively eusocial species, colonies have annual life cycles and populations are relatively small, typically a few dozen to a few hundred individuals. There are no morphological differences between queens and workers, but there can be differences in physiology and size. Division of labor for reproduction is achieved by a dominance hierarchy that is established and maintained by direct behavioral mechanisms, including pushing, biting, and physical prevention of egg laying. Aggression is a common occurrence in a primitively eusocial colony. Bumble bee species exhibit a primitively eusocial lifestyle.

In advanced eusocial species, colonies are typically perennial and populations number in the thousands to even millions of individuals. Queens and workers are distinguished by striking morphological differences. In advanced eusocial species, queen inhibition of worker reproduction is achieved by chemical communication—queen pheromones—rather than by direct physical aggression. In advanced eusocial species, the fate of an individual—queen

or worker—is determined before adulthood, and there is far less dominance-related aggression among individuals than in other animal societies. This sets the stage for natural selection, acting on the phenotypes of colonies, to fashion systems of division of labor among groups of highly specialized workers and intricate forms of communication to integrate their activities. Honey bees exhibit an advanced eusocial lifestyle.

Several aspects of eusociality contribute to the value of the honey bee as a commercial pollinator: (1) Perennial colonies result in large forces of foraging worker bees, especially early in the growing season, when pollination is required for many crops. Noneusocial species, with annual population cycles, have far smaller populations early in the growing season. (2) Foraging in honey bee colonies is based on division of labor. There is an age-related division of labor among worker honey bees, which is based on a process of behavioral maturation (Robinson, 1992). After working in the hive for 2 to 3 weeks, worker honey bees specialize in foraging for the remainder of their 4- to 7-week adult life. They take about 10 foraging trips per day and log up to 800 km over the course of their foraging career (Winston, 1987). Workers become more efficient at foraging with experience (Dukas and Visscher, 1994), which likely increases their efficacy as pollinators. (3) Foraging in honey bee colonies also is enhanced by communication. Foragers communicate the location of particularly rewarding food sources by means of the famous “dance language,” elucidated by Nobel laureate Karl von Frisch (1967), the only nonprimate symbolic language. Honey bees are thus able to rapidly and effectively direct their foraging force toward a particular field or orchard in bloom. This can enhance pollination by mobilizing a large group of foragers during what is sometimes a relatively short window of opportunity. Pollination often is constrained temporally by floral phenology or adverse weather conditions that limit bee flight (Delaplane and Mayer, 2000). Other traits that enhance the value of *A. mellifera* as a pollinator are described in the section entitled “Honey Bees (*Apis mellifera*)” in this chapter.

Other species of bees display levels of sociality that are intermediate between solitary and eusocial. “Communal” species nest in aggregations but do not display any of the three defining traits of eusociality. *Megachile rotundata* nests in aggregation, which facilitates their use as an actively managed pollinator. “Quasisocial” species display cooperative brood care, but no reproductive castes or generational overlap. “Semisocial” species display cooperative brood care and reproductive castes, but no generational overlap. Some species exhibit different levels of sociality during different phases of the colony lifecycle. A bumble bee colony, for example, is established by a single individual, acting in a solitary manner. When the first brood emerges and assumes responsibility for all colony activities except egg laying, the colony then becomes primitively eusocial. Bumble bee colonies are most valuable for pollination during the eusocial phase, when they have an active group of worker foragers.

efficiency of pollination by ensuring that compatible pollen is transferred among conspecific flowers when needed.

Perhaps of greatest significance to the economic importance of *A. mellifera* is that apiculture—the management of honey bees—is a highly developed discipline that has made bees and beekeeping equipment widely available. Honey bees have been used in North America to provide pollination services for crops in bloom in extensive areas. Typically, one-quarter to one-third of workers in a colony during flight season are foragers. Honey bees can be concentrated in very high densities, which are required for effective pollination in large monocultures with extremely high floral densities, and they can be transported by truck to any location at any time crops are in bloom. Finally, because honey bees can be cared for and maintained by humans, they are buffered to some extent from declines in environmental quality.

Honey bee populations have followed different trends in the three North American nations. In the United States, data from the USDA National Agricultural Statistics Service (NASS) reveal declines in the number of honey bee colonies producing honey during 1947–1972 and 1989–1996 (Figure 2-1) (USDA-NASS, 1995, 1999, 2004a, 2005, 2006a). Overall, the number of managed colonies dropped from 5.9 million in 1947 to 2.6 million in 1996–2004. That number fell again in 2005 to 2.4 million. The decline from 1985 to 1996 is likely linked to the occurrence of the tracheal mite,

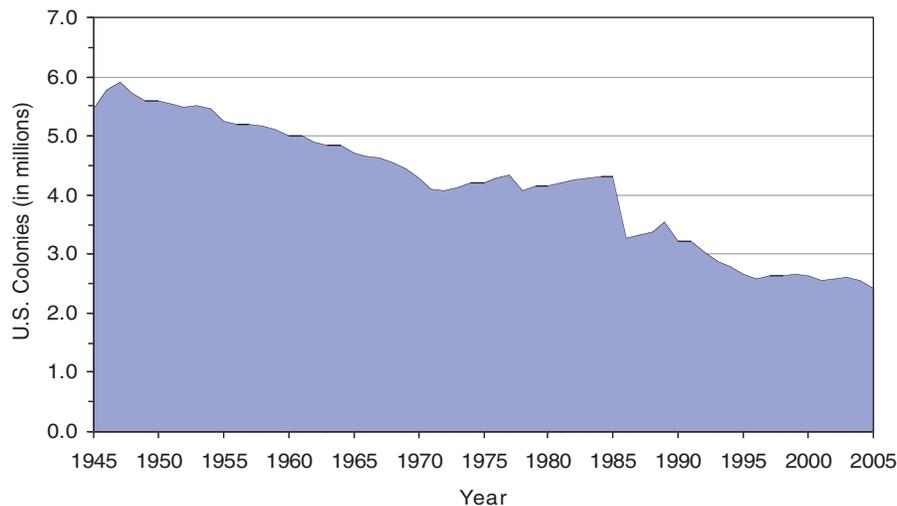


FIGURE 2-1 U.S. honey bee colonies, 1945–2005. Data compiled from USDA-NASS (1995, 1999, 2004a, 2005, 2006a).

Acarapis woodi (first detected in 1984) and to the *Varroa destructor* mite (first detected in 1987) (Chapter 3). The precipitous drop between 1985 and 1986 also is attributable to a change in NASS survey methods that could represent a statistical artifact. After not collecting data from 1982 to 1985 (official data were based on estimates only), NASS changed its surveys to exclude beekeepers who had fewer than five colonies.

Assuming that estimates of honey bee pollination activity in agricultural crops would be improved by more accurate information on total commercial honey bee colony numbers, the U.S. data have four limitations, most of them linked to the NASS focus on honey production. First, the surveys count only honey bee colonies from which commercial honey is harvested; those that exclusively provide pollination services are not counted. Second, the same hives can be counted in several states if commercial honey is harvested in more than one state. Third, annual data are no longer collected on the number of colonies held by beekeepers who own fewer than five hives. Finally, no data are collected on colony health, a factor that has become more important since the parasitic mite invasions of the 1980s (Chapter 3). NASS also surveys beekeeping operations every 5 years for its census of agriculture (USDA-NASS, 2004a). The 2002 census included all honey bee colonies and reported them “in the county where the owner of the colonies’ largest value of agricultural products was raised or produced” (USDA-NASS, 2004a), thus addressing the first three limitations above. However, the agricultural census data are taken less frequently and the variable definitions are incompatible with the annual honey survey data.

In contrast to the declines in the United States, Canada had important periods of growth in honey bee colony numbers between 1955 and 1986 and from 1996 to 2005 (Figure 2-2) (Statistics Canada, raw data and 2006). As in the United States, there was a decline after the period of mite invasions in the late 1980s, and the Canada-U.S. border was closed to the importation of live bees in 1987 to prevent the spread of mites from the United States to Canada (Saskatchewan Agriculture and Food, 2004). Statistics Canada collects data on honey bees kept for pollination and on those that produce honey (Statistics Canada, 2006), but there are some inconsistencies in data collection practices across provinces.

Honey bee colony data from Mexico, available only for 1990–2003, show a decline in the total from 2.1 million colonies to 1.7 million colonies between 1990 and 1997 (SIAP, 2005). With minor fluctuations, colony numbers remained stable at 1.7 million during 1997–2003. Mexican honey production data are available for a longer period, 1980–2002, but those data do not show any clear trend. Honey production in the principal states of Yucatán, Campeche, Veracruz, Jalisco, Guerrero, and Quintana Roo has fluctuated from 42,000 to 75,000 metric tons, leveling off at 57,000–59,000 metric tons in 2000–2004 (Ortega-Rivas and Ochoa-Bautista,

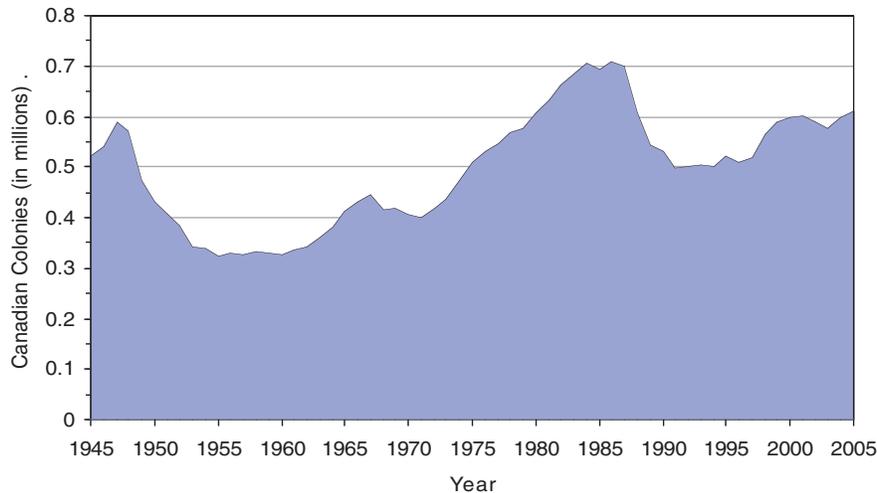


FIGURE 2-2 Canadian honey bee colonies, 1945–2005. Data compiled from Statistics Canada (raw data and 2006).

2004; SAGARPA, 2005). Details on data collection procedures were not available.

In contrast to honey bees reared for commercial pollination, feral honey bees are not well studied (Buchmann and Nabhan, 1996; Hoopingarner, 1991). Because honey bees are not native to North America, feral honey bee populations (like those that are actively managed) represent races introduced to the United States from eastern and western Europe and from Africa since the 1620s (Schiff et al., 1994). Schiff et al. (1994) studied the genetic diversity of feral honey bee populations in the southern United States and found that 61 percent of the 692 colonies assessed were maternal descendants of the European races most commonly used for commercial pollination.

Few studies have examined the population status of feral honey bees over time. The USDA Carl Hayden Bee Research Center has data on the survival of feral honey bee colonies in southern Arizona that span 19 years (Loper et al., 2006). Loper found that feral honey bee colonies in this area were decimated by tracheal mites in 1990 and varroa mites in 1995 (Loper, 1995, 1996, 1997). In 2002, Seeley (2003) repeated a survey of feral honey bee colonies of Arnot Forest, New York, that he conducted with Visscher in 1978 (Visscher and Seeley, 1982). He found that the number of honey bee colonies was about the same in 1978 and 2002. Kraus and Page (1995) studied the spread of varroa mites within California's population of feral honey bees. In 1990, a sample of bees from 208 colonies located in feral hives revealed no varroa mites. In 1993, a survey of 124 of the same

feral hives revealed 75 percent of these colonies no longer existed, and all surviving colonies were infested with varroa. The proximity of these feral colonies relative to commercial apiaries led Kraus and Page (1995) to suggest that the mites moved from commercial to feral colonies. Other than these studies, the committee is not aware of other surveys of feral honey bee colonies in North America.

Bumble Bees (Bombus spp.)

Approximately 239 bumble bee species are known worldwide (Williams, 1998), 49 of them in the United States. The 41 species in Canada are also all found in the United States. Twenty species are known in Mexico, nine of them also present in the contiguous United States (R.W. Thorp, University of California, Davis, presentation to the committee, January 14, 2006; personal communication, March 2006). Some species of bumble bees (*Bombus impatiens* and *B. occidentalis*) have been managed primarily for pollinating greenhouse tomatoes (Dogterom et al., 1998). In contrast with managed honey bee colonies (*Apis mellifera*) in the United States and Canada—for which agricultural monitoring agencies often have long-term records of honey bee colonies (Figure 2-1)—data on managed bumble bee colonies are not collected in the United States, Canada, or Mexico.

Native bumble bees pollinate wild flowers and serve as alternative or complementary pollinators for some crops, such as watermelon and cucumber (Stanghellini et al., 1996a,b). Although many native bumble bee species in the United States were once common, entomologists and naturalists have been noting declines and regional absences of some species within the past decade. The Xerces Society for Invertebrate Conservation has placed four bumble bee species (Appendix H) on its Red List of at-risk pollinator insects of North America (Shepherd et al., 2005).

Bombus (Bombus) franklini (Frison, 1921), the Franklin bumble bee, is (or was) an endemic species with the most restricted geographic range of any bumble bee in North America and possibly the world (Williams, 1998). Its range, known at one time to span from southwest Oregon to northwest California, encompasses a distance of 241 km north to south and 112 km east to west. Within that area, *B. franklini* could be found at elevations from 162 m in the north to above 2,340 m in the southern portion of its historic range. *B. franklini* is thought to have become extinct recently in its native range of the U.S. Pacific Northwest (Buchmann and Ascher, 2005; Shepherd et al., 2003, 2005). Thorp (2003, 2005) first began to notice and document a precipitous decline in *B. franklini* at numerous localities in 1988. Extensive searching by R.W. Thorp and his colleagues over the last 4 years has failed to re-locate *B. franklini* populations or individuals across that region (Thorp, 2003). *B. franklini* is now treated as a “species of concern” or a “special

status species” by the U.S. Fish and Wildlife Service, the California Natural History Data Base, and the Oregon Natural Heritage Information Center. It also appears on the Xerces Society Red List (Appendix H; Shepherd et al., 2005).

B. occidentalis, at one time commonly observed in central California, began in the late 1990s to disappear from most of its known geographic range. Thorp (2003, 2005) conducted extensive searches for *B. occidentalis* and reported that it is now extremely rare in habitats where it was formerly common. The species is still present in some parts of its range, such as the Colorado Rocky Mountains; it is still relatively common near the Rocky Mountain Biological Laboratory as of 2006 (D. Inouye, University of Maryland, personal observation, 2006).

B. affinis apparently disappeared from northern New York state about 1998 and from southern New York before 2004 (Day, in preparation; J. Ascher, American Museum of Natural History, personal communication, March 2006). John Ascher of the American Museum of Natural History reports that *B. affinis* was common on the Cornell University campus between 1996 and 1998, but that he and other entomology students and faculty have not observed it since 2001. Despite collecting more than 1,200 bumble bees in the Black Rock Forest of New York during 2003, Giles and Ascher (2006) failed to find any specimens of *B. affinis*.

Because there is no long-term monitoring or corresponding baseline data for bumble bees or other species of wild non-*Apis* bees in the United States, Canada, or Mexico, the population status of bumble bees cannot be determined definitively in North America. The United Kingdom, in contrast, has a long and well-established tradition of monitoring by scientists and naturalists. Extensive standardized monitoring protocols are followed across a grid system covering the entire United Kingdom. The Bees, Wasps and Ants Recording Society was established in 1978 expressly to allow “anyone of any age or experience with an interest in aculeates” (ants, bees, and stinging wasps) to contribute to a recording scheme designed to obtain “proper, well coordinated data on the distribution and habitats of many species in order to support conservation programmes, ecological research, and to promote effective conservation strategies on a national basis” (<http://www.searchnbn.net/organisation/organisation.jsp?orgKey=222>). The ALARM project (Assessing Large Scale Risks for Biodiversity with Tested Methods) was established in 2004 with the objective of assessing changes in the richness, abundance, and distribution of pollinators across Europe (Box 2-3). This project and several other studies show that decline in species richness, frequency, and distribution of bees is evident (Box-2-4; Goulson et al., 2005; Westrich 1989, 1996) if these parameters are carefully monitored or observed. Records of species richness, frequency, and distribution of bees in North America are few in number.

BOX 2-3
The ALARM Project
Changes in Bee and Flower Fly Richness, Abundance, and
Distribution Documented

In 2004, the ALARM project (Assessing Large Scale Risks for Biodiversity with Tested Methods) was initiated and funded as part of the United Nations Food and Agriculture Organization. Details of the program are presented in Chapter 5, but one component relevant to this discussion is the effort to quantify distribution shifts in keystone pollinator groups across Europe. ALARM researchers conducted an extensive before-and-after 1980 repeat survey of native bees and flower flies in the United Kingdom and the Netherlands (Biesmeijer et al., 2006). Each country was divided into 10 x 10 km grid cells and species richness and abundance were analyzed on the basis of more than 500,000 authenticated records. A landscape-level rarefaction analysis (Colwell et al., 2004; Krebs, 1999; Magurran, 2004) was conducted from the United Kingdom and Netherlands data sets and analyzed with EstimateS 7.5 software (Colwell, 2005).

The results of these first comprehensive national surveys of pollinators show widespread decline of bees and syrphid flies. Species richness of bees declined in about 40 percent and 60 percent of the grid cells in the United Kingdom and the Netherlands, respectively. In the United Kingdom, 18 percent of the grid cells showed increases and 45 percent had the same species richness. The national data from the two countries allowed researchers to ask whether individual pollinator species were changing in distribution and abundance. Of the 229 bee species assessed in the United Kingdom and the 201 species assessed in the Netherlands, more showed declines in abundance from before to after 1980 (based on the total number of times each species was recorded across all grid cells in which they were present in those two periods) than stayed stable or decreased. In the Netherlands, the number of species that showed area loss (range contraction) was substantially higher than the number that showed area gain (range expansion), with an overall significant decrease in occupancy. In contrast, no clear trends in range changes were observed in the United Kingdom. When abundance and range changes were considered together, there were statistically significant declines in native bees in the United Kingdom and the Netherlands (Biesmeijer et al., 2006). The findings are consistent with studies of status for butterflies (Asher et al., 2001; J.A. Thomas et al., 2004), for bumble bees (Rasmont et al., 2006), and for native European bees (Banaszak and Kosior, unpublished data; Sároszpataki et al., 2005).

SOURCE: Biesmeijer et al., 2006.

BOX 2-4

European Bee Surveys and Population Declines

A United Nations Food and Agriculture Organization report, *The Survey of Wild Bees (Hymenoptera, Apoidea) in Belgium and France* (Rasmont et al., 2006), presents evidence of pollinator declines among diverse taxa of bees native to those countries during the past 30 years. The Belgian Mons and Gembloux government laboratories published their first report on native bees of Belgium and France in 1980 (Leclercq et al., 1980), listing 13 species of the superfamily Apoidea at risk in Belgium, Luxembourg, and northern France. A subsequent report (Rasmont and Mersch, 1988) presented information on the faunistic drift of Belgian bumble bee species; that report cites the first red list of threatened insects in the Belgian fauna. The 1988 report was updated and revised in 1993 (Rasmont et al., 1993) to include general findings about the entire Belgian bee fauna of more than 300 species. After 1993, research teams at the two Belgian laboratories expanded their bee survey efforts to other areas and countries, including France (Pauly, 1999; Rasmont and Adamski, 1995; Rasmont and Gaspar, 2002; Rasmont et al., 1995), Morocco (Rasmont and Barbier, 2003), Turkey (Rasmont and Flagothier, 1996), and even Madagascar (Pauly et al., 2001). Rasmont and his colleagues have prepared biogeographic, faunistic surveys and taxonomic revisions of bee genera at continental scales (Andrenidae: Patiny, 1998; Patiny and Gaspar, 2000; Anthophoridae: Terzo and Rasmont, 2004; Melittidae: Michez et al., 2004a,b; Terzo and Ortiz-Sanchez, 2004).

To date, 360 species of bees have been reported in Belgium; of these, 330 species of solitary bees (Apoidea) were documented as occurring within Belgium between 1900 and 1992 (Rasmont et al., 2006). In that period, 91 species (25.2 percent) were decreasing in abundance, 145 (40.2 percent) remained relatively stable, 39 (10.8 percent) had expanded their ranges, and 85 species (23.5 percent) were placed in an undetermined situation as rare species. These data were collected from more than 48,000 records and 79,765 specimens. Results from the study published by Rasmont and colleagues (2006) confirmed that 13 of the same species were decreasing as had been reported by Leclercq et al. (1980). Rasmont and colleagues (2006) also reported a sharp contraction in most cleptoparasitic (cuckoo bee) species and hypothesized that their bee host species had declined. The report also discussed a decline among mason bees (*Osmia* spp.) that use snail shells as nesting substrates. The same observation had been reported earlier by Westrich (1990). With respect to the overall pattern of change, Rasmont and colleagues (2006) state:

In an untouched wild bee fauna, the isolated regression of a long-tongued species could probably be ecologically compensated for by the spontaneous substitution of competing species. However, in the present situation, it is the whole guild that is threatened. Therefore, we may fear that the linked regression of all species will not allow a spontaneous replacement. It is likely that the density and the diversity of these pollinators fall under the population level needed to insure the pollination requirement of many agricultural and horticultural productions. Moreover, the regression of key species would lead to the disappearance of great parts of the wild flora.

Rasmont and colleagues (2006) make a special case to discuss the plight of bumble bees in Europe. They reported a continental decline in abundance in several bumble bee species. The most dramatic case was for *Bombus cullumanus* (Kirby). At the start of the 20th century, *B. cullumanus* was seen as far north as southern Sweden and was abundant in northern Germany, the Netherlands, and England. It had been observed in large cities, such as Brussels and Paris, since the 1950s. By the 1990s, it had disappeared from most of its former range. Today, it can be found only in a few dozen localities in the West and East Pyrénées and in western portions of the Massif Central mountains, and it is now rare wherever it is found (Rasmont et al., 1993). The authors reported that other bumble bees—*B. confusus* Schenck, *B. distinguendus* Morawitz, and *B. sylvarum* (L.), all long-tongued species associated with leguminous floral hosts—also experienced contractions within their respective ranges. A few, however, have actually expanded their ranges. *B. semenoviellus* (Skorikov), originally known from Moscow, can be now found in northern Germany and is expected to colonize the Netherlands and Belgium in the next few years.

Another formerly common, now rare, species is the leafcutting bee *Megachile parietina* (Goeffroy) (= *Chalicodoma muraia* Retzius) in France. Toward the end of the 19th century, when Jean-Henri Fabre was writing his famed *Souvenirs Entomologiques*, this leafcutting bee was common enough to be considered a pest in buildings. It has become rare throughout France, for unknown reasons (Rasmont and Barbier, 2003). *M. parietina* is a visitor to legume flowers, so its population decline could be symptomatic of a larger problem among native leguminous plants and their pollinators in France and Belgium. A rare carpenter bee, *Xylocopa cantabrita* Lepelletier, was formally known only from a few localities in France and Spain. Terzo and Rasmont (2004) relocated that rare bee during recent faunal surveys.

Mexican Stingless Bees (Melipona and Trigona)

Stingless bees, species in the tribe Meliponini, comprise about 400 species found in neotropical and paleotropical forests (Roubik, 1989). These social bees form long-lived colonies, make and store honey, and are important pollinators of forest trees and crops. For millennia, ancient and modern Mayan peoples of southernmost Mexico and neighboring countries have kept the meliponine bees of their tropical forest environments in hollow log hives (“jobones”) in or near villages. Stingless bees have supplied the Maya with honey for food and for medicine and with beeswax as a sealant and art material (Crane, 1999).

Mayan beekeepers have traditionally searched for stingless bee colonies in the low tropical forests of the Yucatán, traveling several kilometers from their villages to locate wild colonies of *Melipona* and *Trigona*. Today, beekeepers must travel even farther into smaller patches of remnant forests of large-diameter trees (used by stingless bees for nesting cavities) to find *Melipona* colonies (Villanueva, personal communication, March 2006). In the past, bee houses with traditional log hives contained dozens or hundreds of colonies, and beekeepers knew how to divide and reproduce colonies (Villanueva-Gutierrez et al., 2005). It is now uncommon to find a beekeeping operation with more than five colonies of *Melipona* in villages near Felipe Carillo Puerto, Quintana Roo (Villanueva-Gutierrez and Roubik, personal communication, March 2006).

Ancient Mayan beekeeping is disappearing because of habitat fragmentation and intensive apiculture. A recent survey (Villanueva-Gutierrez et al., 2005) documented that 93 percent of the managed *Melipona* and *Trigona* stingless bee colonies in the Yucatán Peninsula have been lost during the past quarter-century (Table 2-1). Hurricanes in the past two decades have also decimated feral and managed colonies of Yucatecan stingless bees. Villanueva-Gutierrez and colleagues predict there will be no managed colonies of *Melipona* and *Trigona* in Yucatecan Mayan lands by 2008 unless action is taken to maintain the bee colonies (Villanueva-Gutierrez et al., 2005).

Sixteen species of gentle native bees are found within the Yucatán Peninsula, where they pollinate forest trees, Mayan dooryard gardens, and milpa agricultural lands. There are no studies on population trends of feral meliponines, although Búrquez (2003) examined the distributional limits of meliponines in northwestern Mexico. They are not present in the United States or Canada.

Orchid Bees (Euglossa, Eufriesea, Exaerete, Eulaema)

Orchid bees (family Apidae, tribe Euglossini) constitute a natural group of approximately 250 brilliant metallic-green, blue, and red species from

TABLE 2-1 Number of *Melipona* Hives That Beekeepers from the Mayan Zone (near Felipe Carrillo Puerto, Quintana Roo, Mexico) Have Kept During the Past 54 Years

Name of Mayan Community	Name of Beekeepers or Institutions	Number of Hives Kept Between 1950 and End of 1981	Number of Hives Kept at End of 1990	Number of Hives Kept at End of 2003
Chan Santa Cruz	Delfino Naal	Unknown	8	2
Chan Santa Cruz	Nemesio Pot	Unknown	12	8
Chancá de Repente	Bernardo Peña	42	25	8
Chancá de Repente	Anastasio Perez	Unknown	10	0
Chancá de Repente	Eduardo Yam	Unknown	5	0
Chunyá	Patricio Canul	45	30	8
Felipe Carrillo Puerto	Instituto Nacional Indigenista	0	40	11
Miztequilla	Santiago Pat	Unknown	6	2
Miztequilla	Fernando Yam	40	19	8
Naranjal	Francisco Cimá	25	15	3
Naranjal	Juán Mena	26	12	6
Nueva Loría	Celestino Camal	Unknown	7	2
Nuevo Israel	Ponciano Tun	Unknown	6	0
Palmas	Margarito Tuz	220	5	0
Presidente Juárez	Bernabé Kantún	Unknown	16	4
San Hermenegildo	Humberto Ku Cauichl	60	40	0
Santa María	Francisco HuiCab	50	37	7
Señor	Doroteo Pech	22	18	0
Señor	José Pott	Unknown	6	0
Tihosuco	Pedro Cahun Uh	Unknown	5	15
Tuzic	Isidro Peña Tuz	200	40	8
X hazil	Modesto Chuc	10	7	0
X hazil	Isaías Cahuich	15	10	0
Yo Actún	Rancho San Martín	Unknown	10	4
Totals		Likely >1000	389	96

SOURCE: Villanueva-Gutierrez et al., 2005.

the neotropical forests of Mexico south into Central and South America (Cameron, 2004; Michener, 2000; Roubik and Hanson, 2004). Although an errant *Eulaema* male was discovered in the United States (Minckley and Reyes, 1996), orchid bees live in neotropical forests and can be found in Sonora and Sinaloa (Alamos region) and farther south, including the rainforests of Quintana Roo, Mexico. Euglossines historically have comprised up to 25 percent of the total bee fauna in many intact neotropical forests, and they are thought to be excellent indicators of disturbance (Roubik and Hanson, 2004; Roubik, personal communication, March 2006). Within intact forests, however, euglossine populations are extremely stable, and some species might even be increasing (Roubik, 2001).

TABLE 2-2 Examples of Bees in North America and Some of the Plants They Visit and Pollinate

Common Name	Scientific Name	Examples of Crop Plants Pollinated
Alkali bee	<i>Nomia melanderi</i>	Alfalfa, clover, mint
Blueberry bee	<i>Habropoda laboriosa</i>	Blueberry
Carpenter bee	<i>Xylocopa</i> spp.	Passion flower, eggplant, pepper
Digger bee	<i>Andrena</i> , <i>Colletes</i> , and <i>Melissodes</i> spp.	Cotton, fruit trees
Alfalfa leafcutting bee	<i>Megachile rotundata</i>	Alfalfa
Blue Orchard bee (a mason bee)	<i>Osmia lignaria</i>	Almond, apple, sweet cherry
Squash and gourd bee	<i>Peponapis pruinosa</i> other <i>Peponapis</i> and <i>Xenoglossa</i> spp.	Squash, pumpkin, gourds
Sunflower bee	<i>Eumegachile pugnata</i>	Sunflower

Other Bees

Other than honey bees and bumble bees, more than 3,500 species of solitary bees pollinate crops and wild plants in North America. Examples of native bee pollinators include alkali bees, squash bees, and leafcutting bees (Table 2-2). A number of native bee species are rare and have narrow geographic ranges or have not been collected for many decades. The Xerces Society Red List for bees is presented in Appendix H, Table H-2.

Ants

All 11,844 named ant species are eusocial, ecologically important insects (Agosti and Johnson, 2005; Hölldobler and Wilson, 1990, 1994; Wilson and Hölldobler, 2005). Common in most plant communities, ants visit plants and collect sugars. Interactions with flowering plants involve mutualisms that include dispersing seeds, visiting extra-floral nectarines, serving as guards against seed predators or herbivores, and in some cases pollinating flowers (Beattie, 1985; Boucher, 1985; Bronstein, 1944a,b; Bronstein and McKey, 1998; Buckley, 1982; Huxley and Cutler, 1991; Janzen, 1985; Rico-Gray and Oliveira, 2006; Thompson, 1982, 1994, 2005; Wilson and Hölldobler, 2005). Although ants are collectively involved in thousands of interactions with plants and are commonly observed on flowers, they pollinate few species (about 20) of angiosperms (Table 2-2; Beattie, 1985; Peakall et al., 1991; Rico-Gray and Oliveira, 2006; Thien and Rico-Gray, 2004). Nevertheless, many ant-plant mutualisms other than pollination greatly increase the reproductive success of plants and ants.

The 20 flowering plants (18 genera, 9 families) pollinated by ants (Table 2-3) occur in a variety of habitats throughout the world. Of the

TABLE 2-3 Plant Species in North America
Pollinated by Ants

Species	References
Caryophyllaceae	
<i>Arenaria tetraquetra</i>	Gómez et al., 1996
<i>Gypsophyla</i>	Gómez et al. 1996
<i>Paronychia pulvinata</i>	Puterbaugh, 1998
Crassulaceae	
<i>Diamorpha smalli</i>	Gomez et al., 1996; Wyatt, 1981; Wyatt and Stoneburner, 1981;
Brassicaceae	
<i>Lobularia maritime</i>	Gómez, 2000
Euphorbiaceae	
<i>Euphorbia cyparissias</i>	Schurch et al., 2000
Orchidaceae	
<i>Mirabilis nyctaginea</i>	Cruden, 1973
<i>Epipactis palustris</i>	Brantjes, 1981; Nilsson, 1978
<i>Maxillaria parviflora</i>	Singer, 2003
Polygonaceae	
<i>Eriogonum pelinophilum</i>	Bowlin et al., 1993
<i>Polygonum cascadenense</i>	Hickman, 1974
<i>Orthocarpus pusillus</i>	Kincaid, 1963

16 subfamilies of ants, the Ponerinae, Myrmicinae, Formicidae, and Dolichoderinae (Grimaldi and Engel, 2005; Wilson and Hölldobler, 2005) are commonly involved in plant interactions (more than 33 genera; antagonistic and mutualistic) (Rico-Gray and Oliveira, 2006).

There are no databases that monitor fluctuations in ant populations. Recent studies, however, have documented population shifts of groups of organisms that include ants (Christian, 2001; Forsy and Allen, 2005; Haugaasen et al., 2003; Morrison, 2002; Richardson et al., 1996; Roberts et al., 2000; Torres and Snelling, 1997). Currently, the Conservation International Tropical Ecology, Assessment, and Monitoring project (<http://www.teaminitiative.org>) tracks litter and ant diversity in Costa Rica (Agosti et al., 2000; J.T. Longino, Evergreen State College, personal communication, October 2005). An excellent source of information on ant databases in general is <http://antbase.org>, a website maintained jointly by the American Museum of Natural History and the Ohio State University.

Wasps

Most of the approximately 100,000 described wasp species worldwide are carnivorous, preying on other insects. Many others are parasites, laying their eggs on or inside immature insects or other living hosts. The large

“digger wasp” family (Sphecidae) contains approximately 9,550 species, most of which are carnivorous, seeking out insect prey to provision their larval cells (http://www.calacademy.org/research/entomology/Entomology_Resources/Hymenoptera/sphecidae/Number_of_Species.htm). Although sphecids are not always hairy or good pollen vectors, many adults that visit flowers to search for nectar might serve as pollinators. Similarly, some species within the large spider wasp family (Pompilidae) seek out flowers for nectar. Their spiny legs pick up and transport the specialized pollinia of milkweed plants (*Asclepias* spp.) and they can be effective pollinators (Kephart and Theiss, 2003). One group of large wasps that has adopted a flower-visiting, pollen-collecting, larval-provisioning lifestyle includes the subfamily Masarinae within the family Vespidae. Two genera (*Pseudomasaris*, with 14 species limited to the western United States, and *Euparagia* with 6 species) are found in the United States. *Euparagia* species visit *Eriogonum* blossoms for nectar, but provision nests with paralyzed weevil prey items. Unlike bees, *Pseudomasaris* wasps actively harvest pollen and nectar and then provision their underground brood cells with pollen or nectar instead of live or paralyzed arthropod prey (spiders, pompilid wasps, weevils). Many masarid species have elongate mouthparts that are specialized for extracting nectar from long tubular blossoms. In the southwestern United States, species of *Pseudomasaris* are oligolectic (their pollen foraging is restricted to particular genera or to a single genus within a plant family), and they provision their nests with pollen and nectar largely from flowers of plants within the families Hydrophyllaceae, Polygonaceae, and Scrophulariaceae. They are principal pollinators of species of beardstongue (*Penstemon* spp.), including the endangered *P. grahamii* (<http://www.epa.gov/fedrgstr/EPA-SPECIES/2006/January/Day-19/e363.htm>), *Phacelia*, *Hydrophyllum*, and *Eriodictyon*. Pseudomasarines are important to the ecology of these wildflowers, and they play ecosystem service roles in the southwestern United States and Mexico. Within the southwestern United States, several masarid species are restricted to highly localized habitats or have not been collected in decades (Richards, 1963, 1966). *Pseudomasaris micheneri* is known only from the Inyo Mountains of Inyo County, California (Westgard Pass), and only from collections made during the 1930s and 1940s. It has not been collected since then. *Pseudomasaris macneilli* is known from only two locations in northern California (Trinity Alps) and one location in Utah. Those collections were made during 1951 and 1961. Similarly, *Pseudomasaris macswaini* has a localized distribution and could be at risk (Richards, 1963, 1966). Further exploration and collection in known habitats when *Phacelia* and other floral hosts are in bloom will be necessary to determine the current status of masarine populations in North America.

An example of pollinator-plant interdependence involves the so-called fig wasps. The term “fig wasp” has been broadly applied to many plant-

feeding chalcid wasps (Chalcidoidea) that have mutualistic relationships in inflorescences (synconia) of fig trees (*Ficus*, Moraceae). There could be several hundred such species, although many are still undescribed (Weiblen, 2002). Formerly, these wasps were all placed within the family Agaonidae. Molecular studies and DNA sequences indicate that the five families containing fig wasps (Agaonidae, Eurytomidae, Pteromalidae, Ormyridae, and Torymidae and the subfamilies Epichrysomallinae and the Sycophaginae) are not closely related (Campbell et al., 2000; Machado et al., 1996; Rasplus et al., 1998). The Sycoecinae, Otitesellinae, and Sycorctinae have been placed in the Pteromalidae, which leaves only the truly fig-pollinating wasps in the Agaonidae. Forty-seven genera, comprising approximately 800 species worldwide of fig-loving wasps are recognized as pollinators of *Ficus* species. There are 21 species of *Ficus* in Mexico, two in the United States (Florida), and none in Canada. Unlike most flowering plants, which can be pollinated by a guild of pollinators and floral visitors, each *Ficus* species typically is primarily pollinated by one, or sometimes two, species of agaonid fig wasps (Weiblen, 2002). Some wasps associated with figs, but not typically thought of as pollinators, can enter through fig ostioles—small openings in the fruit—to effect pollination (Jousselin et al., 2001).

Originally native to western Asia and the Mediterranean, the edible fig (*Ficus carica*) is the only species cultivated commercially for fruit production. In the United States, California dominates, with 98 percent of U.S. fig production (60,000 tons), although according to the USDA Economic Research Service (ERS), figs are grown commercially in at least 14 states (USDA-ERS, 2004).

Twenty-one species of *Ficus* are indigenous to Mexico; none of these tropical species can survive unaided in Canada. Two native *Ficus* species are known in the continental United States, occurring naturally in southern Florida (*F. aurea* and *F. citrifolia*). Only five species of agaonid fig wasp are known from Mexico, although unreported species could occur there (Noyes, 1998; Rasplus et al., 1988; J.Y. Rasplus, personal communication, January 2006). Despite the importance of fig wasps to pollination of *Ficus*, there are no published studies documenting population trends in this group.

Beetles (Order Coleoptera)

With about 350,000 described species, beetles (Coleoptera) constitute the largest insect order (Grimaldi and Engel, 2005). Beetles often are ignored as pollinators because both the larvae and the adults of so many species destroy the reproductive organs of wild and domesticated seed plants (Borror et al., 1989). However, beetle pollination is believed to have contributed to the pollination of different lineages of flowering plants for over 120 million years (Bernhardt, 1999, 2000) as shown by the preponderance of beetle pol-

ination in surviving species of basal (magnoliid) angiosperms (Bernhardt and Thien, 1987) and in reconstructions of flower and beetle fossils (insects that belonged to still extant lineages associated with pollen consumption).

In a review of the international scientific literature published between 1906 and 1999, Bernhardt (2000) reported that 34 families (representing some 170 discrete species) of flowering plant contain at least one species pollinated primarily by beetles. Another 79 generalist species distributed within 22 families of flowering plants are pollinated by beetles with other animals, including flies, bees, and birds. Pollinating beetles come from at least 27 families within the order. Beetle behavior on flowers varies according to insect species and sex, and some effect pollination while searching for edible rewards (nectar, pollen, starchy food bodies).

The number of pollinating beetle species cannot be estimated—another result of the acknowledged taxonomic impediment (Box 2-1). Knowledge of known beetle species as effective pollinators of U.S. and Canadian vegetation continues to lag behind information about native bees, bats, and birds in the two countries. An estimated 52 U.S. and Canadian plant species are pollinated by beetles (Table 2-4). However, similar estimates are not available in Mexico, and the role of North American flower-visiting beetles as pollinators has yet to be assessed.

Beetle pollination is usually associated with tropical latitudes (reviewed by Bernhardt, 2000). The extent of beetle pollination within the flora of the United States, Canada, and northern Mexico is open to speculation; few studies confirm that beetles contact both receptive pistil tips and pollen-shedding anthers while they forage or find mates (Table 2-3). The role of beetles as pollinators of temperate, North American flora differs by plant geography so that the role a beetle species plays in pollination of temperate, North American flora could change with the distribution of the plant species. In the Southeast, most yellow pond lilies (*Nuphar*) are pollinated by the chrysomelid beetle, *Donacia crassipes* (Schneider et al, 1977). As this genus of water lily has expanded its distribution northwards (it also has been introduced into European water ways), it is pollinated by insects in other orders (Herring, 2003; Lippok and Renner, 1997; Renner and Johanson, 1995).

There are no beetle-pollinated crops in Canada or the United States, unless the recent attempts to domesticate and commercialize fruit production in American species of paw paw (*Asimina* spp.; Norman and Clayton, 1986) are considered. Most *Annona* spp. sold as custard apples, sugar apples, or soursops are beetle pollinated (Gottsberger, 1989a,b), as is *Myristica fragrans* (Armstrong, 1986), the source of the commercial “sister” species, nutmeg and mace.

In the United States and Canada, beetle pollination is economically important in the context of significant numbers of annual and bulbous or-

TABLE 2-4 An Illustrative List of Indigenous Beetle-Pollinated Plants of Canada and the United States (Common Names of Plants are in Parentheses)

Plant Genus	Taxa of Pollinating Beetles	Other Pollinators	References
<i>Asimina</i> (paw paws, 8)	<i>Euphoria sepulchralis</i> <i>Trichius spp.</i> <i>Trichotinius lunulatus</i> <i>T. piger</i> <i>T. rufobrunneus</i> <i>Typocerus zebra</i>	<i>Bombus</i> , flies	Kral, 1960; Norman and Clayton, 1986
<i>Calycanthus</i> (W. spice bush, 1)	<i>Calopterus truncatus</i>	Staphylinid beetles	Grant, 1950
<i>Calochortus</i> (mariposa lilies, 26)	<i>Acanthoscelides</i> sp. <i>Acmaeodera</i> sp. <i>Anastranglia</i> sp. <i>Anthaxia</i> sp. <i>Anthrenus</i> sp. <i>Brachysomida</i> sp. <i>Cryptorhorphalum</i> sp. <i>Diabrotica</i> sp. <i>Emmenotarsus</i> sp. <i>Eschatocrepis</i> sp. <i>Eutrichopterus</i> sp. <i>Hippodomia</i> sp. <i>Judolia</i> sp. <i>Listrus</i> sp. <i>Mordella</i> sp. <i>Mordellistena</i> sp. <i>Nemognatha</i> sp. <i>Trichochrous</i> sp. <i>Trichodes</i> sp.	Bees, flies, and moths	Dilley, 2000
<i>Ipomopsis</i> (gilia, 1)	<i>Trichochrous</i> sp.		Grant and Grant, 1965
<i>Linanthus</i> (linanthus, 1)	<i>Trichochrous</i> sp.		Grant and Grant, 1965

continued

TABLE 2-4 Continued

Plant Genus	Taxa of Pollinating Beetles	Other Pollinators	References
<i>Magnolia</i> (magnolias, 10)	<i>Acmaeodera pulchella</i> <i>Aleochara lata</i> <i>A. sp.</i> <i>Allecula punctulata</i> <i>Amaspis rufa</i> <i>Arthromacra aenea</i> <i>Collops tricolor</i> <i>Copidita thoracica</i> <i>Conotelus sp.</i> <i>Derelemus bicolor</i> <i>Diabrotica duodecimpunctata</i> <i>Epuraea ovata</i> <i>E. duryi</i> <i>Gaurotes cyanipennis</i> <i>Goes debilis</i> <i>Gyrophana sp.</i> <i>Leptaura sp.</i> <i>Macroductylos angustatus</i> <i>Mordella discoidea</i> <i>M. melaena</i> <i>M. octopunctata</i> <i>M. sp.</i> <i>Nitidula sp.</i> <i>Ophistomis bicolor</i> <i>Phyllopage fervida</i> <i>Prionomerus calceatus</i> <i>Satira gagatina</i> <i>Sitophilus oryzae</i> <i>Strangalina luteicornis</i> <i>Staphylinus sp.</i> <i>Trichiotinus innulatus</i> <i>T. piger</i> <i>T. trinotata</i> <i>Typoceros zebra</i>	Bees	Thien, 1974
<i>Nuphar</i> (yellow pond lilies, 3)	<i>Donacia crassipes</i>	Bees, flies	Lippok and Renner, 1997; Schneider et al., 1977
<i>Saururus</i> (lizard's tail, 1)	<i>Trichiotinus spp.</i>	Bees, flies, wasp, and wind	Thien et al., 1999
<i>Xerophyllum</i> (bear grass, 1)	<i>Anastrangalia laetifica</i> <i>Cosmosalia chrysocoma</i> <i>Epicauta sp.</i> <i>Leptaura propinqua</i> <i>Trichodes ornatus</i>	Flies	Vance et al., 2004
Total Plant Species		52	
Total Pollinating Beetles Identified to Species		36	

namental flowers—garden favorites on hybrids and cultivars derived from wild species native to the Mediterranean basin and southern Africa, whose ancestors are beetle pollinated (Dafni et al., 1990; Goldblatt et al., 1998). At least 4 species in the genus *Amphicoma* and the 26 monkey beetle species in 9 genera (*Anisochelus*, *Anisonyx*, *Heterochelis*, *Khoina*, *Lepisia*, *Lepithix*, *Pachynema*, *Peritichia*, and *Scelophysa*) may be involved in pollinating the St. Brigid or poppy anemone (*Anemone coronaria*), orange buttercup (*Ranunculus asiaticus*), red tulip (*Tulipa agenensis*), corn poppy (*Papaver rhoeas*), and the more recently marketed peacock moraeas (*Moraea*), ixias (*Ixia*) and romuleas (*Romulea*). The committee is not aware of any studies on population trends of pollinating beetles.

Flies (Order Diptera)

The true flies (order Diptera) are among the most diverse of the insects, with more than 150,000 species described (Thompson, 2006). Flies are ancient—the oldest fossils are known to have come from the Permian (250 million years ago), and flies might have been the first pollinators (Labandeira, 1998). The group, however, underwent its greatest diversification along with flowering plants from the late Cretaceous onward. Higher flies (suborder Cyclorrhapha) are the result of this radiation and now account for about two-thirds of the extant Diptera (Grimaldi and Engel, 2005). Extant flies are classified into 153 families and 148,416 species, with 124 families and 24,219 species found in Canada, Mexico, and the continental United States (Thompson, 2006).

The state of taxonomic knowledge for higher categories (families and genera) is summarized in the Manual of Nearctic Diptera (McAlpine et al., 1981, 1989). The last assessment of the Nearctic Diptera fauna was done in 1988 (Thompson, 1990) and, according to the results, about two-thirds of all the flies known to occur in America north of Mexico have been named. Unfortunately, fewer than 1 percent of these flies are treated comprehensively in monographs, and fewer than one-quarter of the species have been thoroughly revised. No field guides exist exclusively for flies, and only one digital key has been developed (Carroll et al., 2005). The assessment also noted a decline in specialists in the ranks of graduate teachers at universities and among museum curators.

Most higher flies are flower visitors and many have been documented as pollinators. All of the world's floristic provinces contain at least one plant species pollinated primarily or exclusively by flies, and fly pollination is regarded as second only to bee pollination in the evolution of flowering-plant diversity (reviewed by Larson et al., 2001). Flies as flower visitors (anthophiles) and pollinators have been reviewed by Larson and colleagues (2001). Following from their work (and table) and combined with the number of

species for each group identified as containing pollinators, it is possible to estimate that 17,460 species in North America are flower visitors and likely pollinators (Table 2-5).

Some fly species forage actively in cool, wet climates, so fly pollination could dominate among the flora of the Arctic tundra and the montane-alpine zones of North America (Kearns, 1990; Kevan, 1972). Research published within the past 15 years demonstrates that fly pollination dominates in plant species that are characterized by small flowers that bloom under shade and in seasonally moist habitats. Cacao (*Theobroma cacao*, from which chocolate is obtained) is the best-known example (Young, 1994), but others are in the Iridaceae (Goldblatt et al., 2005) and Saxifragaceae (Goldblatt et al., 2004).

In association with bees, flies appear to contribute to the pollination of several fruit and vegetable crops (Free, 1970), but cacao is the only domesticated plant of major economic significance pollinated exclusively by flies (tropical midges). Cacao is a tropical shrub that cannot be grown in Canada or in most of the United States, but it has been commercially and culturally important to Mexico since the days of the Aztec Empire (Young, 1994).

The dominant pollinators of beargrass (*Xerophyllum tenax*), a montane herb native to the American Pacific Northwest, consist of more than 20 species of flower fly. Licensed collection of beargrass leaves occurs annually for exportation to Europe for the floral craft trade. Harvesters in the Pacific Northwest were paid over \$11.5 million for beargrass in 1989 (Schlosser et al., 1991). A number of garden and potted plants are derived from fly-pollinated species, including birthwort (*Aristolochia*), starfish flower (*Stapelia*), tuberous aroids including the jack-in-the-pulpits (Araceae), and the ancestors of some hybrid gladioli (*Gladiolus*; Bernhardt and Thien, 1987; Goldblatt and Manning, 1999; Proctor et al., 1996). No flies have been truly “managed,” but some flower flies (Syrphidae, genera *Eristalis*, *Syritta*; Jarlan et al., 1997) have been used to pollinate crops in greenhouses.

Knowledge of the distribution and population sizes of North American flies is virtually nonexistent. Although the few published monographs and revisions usually contain summary statements of material examined and, frequently, distribution maps, there are no publicly available databases of substantive specimen data. Similarly, there could be just one long-term program to collect population data for flies, using a Malaise trap at the Rocky Mountain Biological Laboratory in Crested Butte, Colorado. In Europe, however, some groups of flies are actively studied by citizen-scientists. Flower flies (Syrphidae) are very popular with citizen-scientists; syrphids, for example, have been included in the ALARM project (Box 2-2 and Chapter 6).

Population trends cannot be determined without population data for North American flies, although in Europe the ALARM project has

TABLE 2-5 Total Number of Identified Diptera Species and the Estimated Number of Diptera Species That Are Pollinators

Taxon	Number of Species	Estimated Number of Canada, Mexico, or U.S. Pollinators	Level of Taxonomic Knowledge	Level of Ecological Knowledge
Syrphidae	5872	1001	Medium	Medium
Bombyliidae	5009	1095	Medium	Low
Culicidae	3517	289	High	High
Bibionidae	743	111	Medium	Low
Cecidomyiidae	5831	1250	Medium	Medium
Ceratopogonidae	5525	671	Medium	Medium
Psychodidae	2801	172	Low	Low
Chironomidae	6722	1126	Low	Medium
Tabanidae	4295	472	High	High
Rhagionidae	676	118	Medium	Medium
Athericidae	120	6	Medium	Medium
Stratiomyidae	2669	469	Medium	Medium
Asilidae	7166	1286	Medium	Medium
Apioceridae	165	89	High	High
Therevidae	1057	167	High	High
Mydidae	452	90	High	High
Acroceridae	395	68	High	High
Nemestrinidae	255	10	High	High
Empididae	4839	903	Medium	Medium
Dolichopodidae	6742	1459	Medium	Medium
Phoridae	3655	443	Low	Low
Drosophilidae	3863	321	High	High
Lauxaniidae	1844	172	Low	Low
Chloropidae	2841	320	Low	Low
Scathophagidae	291	153	Medium	Medium
Anthomyiidae	1887	709	High	High
Muscidae	4932	774	Medium	Medium
Fanniidae	295	119	High	High
Sarcophagidae	3015	484	Medium	Medium
Calliphoridae	1487	124	Medium	Medium
Tachinidae	9470	2005	Low	Low
Bolitophilidae	54	20	Medium	Low
Diadocidiidae	25	3	Medium	Low
Ditomyiidae	78	9	High	Low
Keroplastidae	837	88	Medium	Low
Lygistorrhinidae	27	1	High	Low
Mycetophilidae	3891	685	Medium	Low
Rangomaramidae	5	0		
Sciaridae	2093	178	Medium	Low

NOTE: Documented population trends are not available for all taxa except for Syrphidae.

documented shifts and declines for several flower fly species in the United Kingdom and the Netherlands (Box 2-3; Biesmeijer et al., 2006). One North American species, the Delhi Sands flower-loving fly (*Rhaphiomidas terminatus abdominalis*; Kingsley, 1996), has been placed on the U.S. Endangered Species List.

Butterflies and Moths (Order Lepidoptera)

With approximately 150,000 species described worldwide (Grimaldi and Engel, 2005), Lepidoptera are among the most species-rich orders of insects, as measured by formally described and documented species. The Lepidoptera include many of the most easily recognized insects, and they are relevant to understanding pollination systems and their origins.

As with most herbivorous insects, butterflies and moths interact with plants during both larval and adult stages, the latter of which are those usually involved in pollination. Although some of the best-studied examples of plant-insect mutualisms involve moths and butterflies (*Heliconius* butterfly, Boggs et al., 1981; Estrada and Jiggins, 2002; yucca moth, Pellmyr et al., 1996; Powell, 1992), obligatory mutualisms are exceptional in Lepidoptera. Although many flowering plants rely primarily on butterflies or moths, most Lepidoptera visit a wide variety of nectar sources. Although lepidopteran pollinators largely are generalists and often transfer only small amounts of pollen, they tend to move longer distances to visit flowers of the same species than do other pollinating insects, such as bees, and thus are important in maintaining gene flow within and among populations (Herrera, 1987, 2000).

The earliest documented North American extinctions of insects involved Lepidoptera (the xerces blue, *Glaucopsyche xerces*), and the Lepidoptera were the bellwethers of the earliest observations of invertebrate species decline in North America (Tilden, 1956). At least some of these extinctions occurred before any information on pollinating capacity of these butterflies was obtained. Butterflies and moths account for a high number of species currently regarded as threatened or endangered in various North American regions and tracked by various state heritage programs (<http://www.nature-serve.org>). Numerous butterfly species are protected under the terms of the Endangered Species Act (Chapter 1) and by state legislation.

Massachusetts, for example, lists 48 Lepidoptera species—nearly half of the invertebrates on its list—as endangered, threatened, or of special concern under MESA (<http://www.mass.gov/dfwele/dfw/nhosp/nhrare.htm>). Most, if not all, of those butterflies and moths have declined significantly in the past 100 years. MESA also lists 10 beetles, 31 dragonflies and damselflies, 8 crustaceans, 7 mussels, 7 snails, and 4 other invertebrates. The large proportion of Lepidoptera listed could be more a reflection of the generally

greater knowledge about them than their larger propensity toward decline (May et al., 1996). Although threatened species legislation varies from state to state, similar trends are widely recognized by scientific and academic communities.

Butterflies

Butterflies and moths often have precise habitat and life history requirements. As is the case for most herbivorous insects, the majority of Lepidoptera generally specialize on three or fewer host plant families for larvae (Bernays and Graham 1988; Farrell and Mitter, 1993; Mitter and Farrell, 1993; Powell et al., 1998). Yet there are significant information gaps about the extent to which plants—economically important and otherwise—rely exclusively on particular lepidopteran species for pollination. Although butterfly larvae tend to be host-specific for food, their activities as adult pollinators are likely to be general. There are notable exceptions; the wild carnation *Dianthus carthusianorum* in Europe, for example, appears to be specialized for butterfly pollination and is visited by five butterfly species, of which two, due to visitation frequency, are principal pollinators (Bloch et al., 2006).

The bay checkerspot butterfly, *Euphydryas editha bayensis* (Nymphalidae), pollinates native plants in North America. Variation in population size of this butterfly has been meticulously documented. It has been the focus of regular census efforts in the Jasper Ridge Biological Preserve near Palo Alto, California, for more than 40 years (Ehrlich and Hanski, 2004), and local population extinctions have been documented for 1991 and 1998 (McLaughlin et al., 2002). Although it is known from other localities (there is a large population in Morgan Hills and a small population near Redwood City), the bay checkerspot was designated as threatened in 1987 and included on the Federal Endangered Species List. It was almost certainly more extensively distributed before the invasion of its habitat by Eurasian grasses (McLaughlin et al., 2002). Local population extinctions of the sort observed for the bay checkerspot have also been documented in the Rhone Valley of Switzerland for *Satyrus ferulae*, which has disappeared from 31 of 62 sites, and *Melanargia galathea*, which has disappeared from 29 of 67 sites, since 1970 (Bloch et al., 2006).

The monarch butterfly, *Danaus plexippus*, pollinates many milkweed and other plant species. It has been the subject of intense interest, in part because of its dramatic ecology (sequestering cardenolides from asclepiaceae host plants and serving as the central model in an extensive mimicry system) and migratory behavior (Halpern, 2001). The Fourth of July butterfly count (known as 4JC in short), an annual monitoring effort undertaken by a broad cross-section of amateurs and professionals, provides insight about fluctua-

tions in monarch populations (Swengel, 1990). Swengel (1995) described population fluctuations.

From 1977 to 1986, the mean number of monarchs per hour in eastern North America varied significantly in only one of nine pairs of consecutive years. From 1986 to 1994, eastern monarchs varied significantly in five of eight year-pairs, with a nearly equal number of increases and decreases. However, the amount of variation within each year-pair was similar for 1977–1986 and 1986–1994 (median difference ca. a factor of 2). Although the Atlantic and midwestern subregions of the eastern population covaried in four of eight year-pairs from 1986–1994, differences between the two subregions sometimes damped fluctuations in the eastern population overall. Data from independent transect surveys in Wisconsin for 1990–1994 agreed with the direction of fluctuations in Wisconsin 4JCs. In 4JCs from 1987–1994 in the Pacific coastal states, monarchs varied less than the eastern population, with a significant increase in 1989 and significant decrease in 1988. However, a nonsignificant decline of an order of magnitude occurred in 1993, and a considerable but smaller increase occurred in 1994. Fluctuations in monarch abundance in eastern North America during 1977–1994 often, but not always, coincided with years affected by major widespread perturbations of typical weather such as the El Niño-Southern Oscillation, major volcanic eruptions, droughts and floods.

Since Swengel's study, other groups have collected data on monarch populations in various locations, and they also have reported fluctuating numbers from year to year (Gibbs et al., 2006; O. Taylor, University of Kansas, presentation to the committee, October 18, 2005).

Results from another Fourth of July Butterfly Count, carried out since 1977 by Arthur M. Shapiro (University of California, Davis), provide information about the variations in populations of 36 butterfly species in the Sacramento Valley. During the 29-year study, 39,614 butterflies were counted; the number of species observed each year ranged from 17 to 30 and the number of individuals from 618 to 2613. The site is a partly channelized perennial stream, its floodplain, and adjacent levees, and it is surrounded by agricultural lands. The results from Shapiro's annual census have been used in a recent analysis (O'Brien et al., in review) to investigate the usefulness of different statistical methods for identifying trends in overall species diversity and in the probability of the presence of individual species. Species diversity declined 38 percent over the study period. Although the decline was detectable by the 13th year, it did not become statistically significant until the 23rd year of the study. Of the 23 species analyzed, 8 have declined significantly and 11 more show a negative (statistically nonsignificant) trend. Neither abundance nor diversity was significantly correlated with any weather patterns examined, although the weather at the study site has warmed significantly over the past 30 years. Thus, the cause of the decline

is still unknown, but species that overwinter as eggs or larvae were more likely to decline than those that overwinter as pupae or adults. Most of the species reported as declining also are declining regionally. The results published by O'Brien and colleagues (in review) point out the importance of systematic, long-term monitoring. Because of statistical limitations, the dramatic decline in species numbers reported in the study would have gone undocumented in a census that lasted less than 22 years.

Moths

Moths are underappreciated as pollinators because most of their pollinating activity takes place at night. They are known to pollinate a diverse suite of plants, ranging from cacti (Clark-Tapia and Molina-Freaner, 2004) to orchids (Little et al., 2005) to trees (Lin and Bernardello, 1999). Some moth species have specialized morphological features, such as long proboscides, and behavior that make them excellent pollinators of some plants (Barth, 1985; Proctor et al., 1996). Some plants, such as various species of *Yucca* (Thompson, 1994), are icons of specialized pollination biology. *Yucca* moths (*Tegeticula* and *Pronuba* spp.) are highly specialized pollinators of *Yucca* spp. within desert and chaparral habitats of the United States and Mexico. The adult yucca moth does not feed, but it uses specially modified palps ("tentacles") to gather up a ball of pollen that it places on a receptive floral stigma, ensuring the production of the seeds that larvae eat (Bogler et al., 1995; Faegri and van der Pijl, 1979; Pellmyr et al., 1996; Proctor et al., 1996). Similarly, *Gaura* and *Calylophus* species (Clinebell et al., 2004) and the senita cactus (*Pachycereus schottii*; Fleming and Holland, 1998) are in plant-specific moth pollinator systems that have been intensively studied.

Although a variety of moths are known to be pollinators, the families Geometridae (geometer moths), Noctuidae (owlet moths), and Sphingidae (sphinx moths) are among the best studied. The Sphingidae (Gregory, 1963–1964) and the highly diverse Noctuidae are among the most efficient of the lepidopteran pollinators. Within the deserts of the southwestern United States and Mexico, large fast-flying hawkmoths or sphingids (Sphingidae) are coadapted pollinators of night-blooming *Datura* spp. (Solanaceae) and night-blooming cacti in the genus *Peniocereus* (Raguso et al., 2003). At least 106 species in the temperate North American flora are known to be visited by sphinx moths, including many from the Onagraceae (Grant, 1985). Migratory noctuids feed on the floral nectar of many species of plants (Kevan and Kendall, 1997). Geometrids have been recorded as pollinators of orchids (Thien and Utech, 1970) among other species. There are no data on population trends of moth species.

Thrips (Order Thysanoptera)

The thrips (Thysanoptera) are slender, small insects (generally no more than one millimeter long), arranged into nine families of living species distributed worldwide, largely in the tropics and temperate regions, with a few species in Arctic regions (Lewis, 1997; Mound, 1997). Checklists of adult thrips have been produced by Stannard (1957, 1968) for North America.

Thrips feed on a variety of plant tissues, including pollen, fungal mycelia, and spores, and they also are predatory (Grimaldi and Engel, 2005; Kirk, 1993, 1997). When they feed on pollen, thrips puncture the coat and drain the grains (Kirk, 1984, 1985, 1997). Grimaldi and Engel (2005) note that pollen feeding evolved several times in thrips; they are so numerous on flowers that they can be effective pollinators of a wide variety of plants in nature and agriculture (Ananthakrishnan, 1993; Endress, 1994; Kirk, 1988; Lewis, 1973, 1997; Terry, 1997). Generally, however, they are regarded as minor or secondary pollinators (Kirk, 1997; Lewis, 1973, 1997; Terry, 2001).

As minor pollinators, thrips also pollinate such agricultural plants as beets, beans, onions, and cacao (Kirk, 1997; Lewis, 1973). Although thrips can pollinate plants in the absence of other pollinators, their importance in open-pollinated crops depends on whether other insects pollinate the flowers first (Kirk, 1997). Thrips can enter unopened buds (Mackie and Smith, 1935), but the peak number of thrips can occur after peak visits by other insects (Kirk, 1984). The grooming behavior of thrips contributes to both self- and cross-pollination in plants (Kirk, 1997). As thrips arrange the fringe hairs before and after flight, pollen grains are shed from their bodies (Kirk, 1997). The stigma is prominent in many flowers and because it is used by thrips for take-off and landing, the pollinator thus places pollen directly on the stigma (Kirk, 1997).

Populations of thrips on crops grown in greenhouses and shade houses depend on breeding within the crop (Kirk, 1997). For example, young chrysanthemum plants are rooted from older plants, and when adult female *Frankliniella occidentalis* (western flower thrips) oviposit in apical leaves, growers can inadvertently raise their own pest populations and transport them to other sites in the cuttings (Kirk, 1997). The flower trade is responsible for the worldwide distribution of that thrips species, as well as others (Table 6.2 of Kirk, 1997).

In part because of their size and their more frequent role as herbivorous plant pests and disease vectors (Ullman et al. 1997), North American thrips have not generally been the focus of concern about population decline; no thrips species is currently protected under the provisions of the Endangered Species Act (ESA). Because of restrictions on ESA, it is unlikely that any species that has had an adverse economic impact on a crop species would

be eligible for listing, even if it could be shown that thrips provide essential pollination services (Chapter 6).

Mammalian Pollinators

Bats

Estimates of the number of bat-pollinated plants species in the Americas range from 600 (Neuweiler, 2000) to 1,000 species (Winter and von Helversen, 2001). Most bat-pollinated flowers have intense scents that are different from those pollinated by other animals (von Helversen and Winter, 2003). Sulphur-based compounds are more common in bat-pollinated species than they are in other pollination systems (von Helversen et al., 2000). Given that the scents are produced in many phylogenetically unrelated species of plants, they are likely the result of long coevolutionary associations (Knudsen et al., 1993).

The color of bat-pollinated flowers is normally inconspicuous, from whitish to green or brown. The color reflectance of the flower itself probably would not be a strong attractant for bats, because most bats are considered color-blind (Jacobs, 1992), although some species might see some color (von Helversen and Winter, 2003). Ultraviolet clues in several bat-pollinated flowers (notably on columnar cacti) prompted studies of bats' ability to detect ultraviolet radiation. Von Helversen and Winter (2003) reported that *Glossophaga soricina* is highly sensitive to ultraviolet light. Other characteristics of bat-pollinated flowers include an outward-facing position at the edge or away from the plant's foliage, thereby facilitating the bats' access. Most bat-pollinated flowers are large, with sturdy petals and exposed stamens and pistil. They generally open at night, and many open only for a single night. The protein content in the nectar of bat-pollinated flowers is greater than it is in flowers pollinated by insects, and those plants generally have more nectar (Neuweiler, 2000). Plant families recognized for their many bat-pollinated species include Agavaceae, Bignoniaceae, Bombacaceae, Cactaceae, Caesalpiniaceae, Chrysobalanaceae, Convolvulaceae, Cucurbitaceae, Fabaceae, Malvaceae, Marcgraviaceae, Mimosaceae, Musaceae, Pandanaceae, and Tiliaceae (Neuweiler, 2000), although as many as 27 plant families in the New World have bat-pollinated species (Vogel, 1969). Most of those groups are tropical, and the number of bat-pollinated species increases as latitude decreases (Heithaus, 1982; von Helversen and Winter, 2003).

There are at least 12 species of pollinating bats in North America, including southern Mexico (Baker et al., 2003; Ceballos et al., 1997; Medellín et al., 1997). The most prominently recognized—by virtue of their conservation status—are the three long-distance migratory species: the

lesser long-nosed bat (*Leptonycteris curasoae*), the Mexican long-nosed bat (*L. nivalis*), and the hog-nosed bat (*Choeronycteris mexicana*). Few population data are available for pollinating bats in North America, given that populations are difficult to survey, few people are qualified to survey them, and few people study them. Most population data take the form of isolated reports that indicate local trends in abundance rather than precise estimates of population size. Information on both species of *Leptonycteris* (Ceballos et al., 1997; Fleming, 2004; Fleming and Nassar, 2002; Fleming et al., 2001a; Galindo et al., 2004; Moreno-Valdez et al., 2004; Stoner et al., 2003) covers regions of western, northwestern, and central Mexico and the researchers have presented data on population dynamics that cover only relatively short periods. An effort to monitor and assess the status of *L. curasoae* is being centralized by the Arizona Game and Fish Department (http://www.azgfd.gov/w_c/edits/documents/Leptcuye.fi.pdf), and the Program for Conservation of Mexican Bats has been compiling information on this and other species for several years (Medellín, 2003; Medellín et al., 2004).

Pollinating bats can be divided into two behaviorally functional groups: species restricted to the tropical regions of southern Mexico (*Glossophaga*, *Hylonycteris*, *Choeroniscus*, *Anoura*, *Lichonycteris*, *Musonycteris*) and those that migrate, moving from central and southern Mexico to northern Mexico and the southern United States (Ceballos and Oliva, 2005; Reid, 1997). All pollinating bats provide important services for many species of North American plants. Many species of columnar cacti, species of *Agave*, trees in the family Bombacaceae, and many other plants rely heavily on bats to carry out sexual reproduction. Agaves are economically important throughout Mexico, but particularly in western regions where they are used for the production of tequila. Tequila production does not, however, depend on pollination by bats. By virtue of their common asexual mode of reproduction, agaves are planted from shoots associated with adult plants, and their flowering is prevented by premature harvest. Nevertheless, bats could be necessary to promote genetic diversity for the long-term viability of commercially grown agaves (Arizaga et al., 2002; Dalton, 2005; Rocha et al., 2005; Valenzuela-Zapata and Nabhan, 2004).

Some other economically important plants linked to bat pollination are the balsa tree (Bombacaceae: *Ochroma pyramidale*), ceiba (*Ceiba pentandra*), and many columnar cacti whose fruits are used and commercialized fresh or dried, or processed into jams, jellies, and candies (*Neobuxbaumia* spp., *Pachycereus* spp., and others) (Bawa, 1990; Watson and Dallwitz, 1992). Ecologically important plants, such as the cardon (*Pachycereus pringlei*), saguaro (*Carnegiea gigantea*), and other columnar cacti, vary in their reliance on bats (Fleming et al., 2001b; Grant and Grant, 1979; Valiente-Banuet et al., 1996). Some populations of these cacti are frequently pollinated by white-winged doves (*Zenaida asiatica*), several species

of hummingbirds, sphingid moths, bees, or beetles (Fleming et al., 2001b; Grant and Grant, 1979; Valiente-Banuet et al., 1996) on the day after their nocturnal anther dehiscence.

The genus *Glossophaga* has four North American species, all present in tropical Mexico. Three of them have wider distribution, extending into Central and South America, and one, *G. morenoi*, is endemic to the dry tropical forest of western Mexico. Two species, *G. commissarissi* and *G. soricina*, are widespread and common and do not seem to face any threat; the other two tend to be locally rare (Ceballos and Oliva, 2005; Reid, 1997). No population estimates or trends have been obtained, but neither is considered to be facing conservation threats by the Mexican government and neither appears on the International Union for the Conservation of Nature and Natural Resources/The World Conservation Union Red List of threatened species (<http://www.iucnredlist.org/>).

Leptonycteris curasoae and *L. nivalis* are migratory species considered threatened in Mexico and endangered in the United States. Their listing in the United States was prompted by surveys in some known roosts that indicated severe declines (U.S. Fish and Wildlife Service, 1988, 1994; Wilson et al., 1985), although subsequent studies suggested that the declines might not have been as severe as originally thought (Cockrum and Petryszyn, 1991). In Mexico, the species was listed as threatened when some winter maternity roosts (the species has a summer and a winter reproductive pulse) were found severely depleted; much of its original habitat in western and central Mexico has been destroyed for tourism and agricultural development (SEMARNAT, 2002). The Program for Conservation of Mexican Bats has monitored between 7 and 20 roosts per year, documenting population stability or growth, and noting temporary declines in some years (Medellín, 2003; Medellín et al., 2004).

Another migratory species listed as threatened in Mexico, but not in the United States, is the hog-nosed bat, *Choeronycteris mexicana* (SEMARNAT, 2002). Although there are no reliable population estimates, since 1906, fewer than 1,500 individuals have been documented throughout the species' range (Cryan and Bogan, 2003). In contrast with the long-nosed bats, this species roosts in small numbers, typically about 12 bats per roost. Because roosts tend to be scattered widely over landscapes, surveys are difficult (Arroyo-Cabrales et al., 1987; Cryan and Bogan, 2003; Tuttle, 2000).

Two of the four North American *Glossophaga* species are very abundant (Ceballos and Oliva, 2005; Reid, 1997), and there is no evidence of decline. Although the one species endemic to Mexico appears to be less common, there are no population estimates that permit a firm assessment of status.

The banana bat (*Musonycteris harrisoni*), a rare species that appears to be highly specialized, as evidenced by its extremely long snout and tongue,

is endemic to western Mexico, from Jalisco to Oaxaca. Fewer than 70 individuals have ever been observed, and only 3 roosts with 3 individuals or fewer have been reported (Télez and Ortega, 1999). The species is considered threatened by the Mexican federal government (SEMARNAT, 2002).

The tailless bat (*Anoura geoffroyi*) is widespread in the southern half of Mexico and occurs frequently at medium elevations—1,000–2,500 m above sea level—and also, rarely, at lower elevations. Although this species is not very common, it is not thought to be facing any threats (Ceballos and Oliva, 2005; Reid, 1997). No population estimates are available.

Three well-recognized pollinator species, *Hylonycteris underwoodi*, *Choeroniscus godmani*, and *Lichonycteris obscura*, tend to be rare. The former two have a wide distribution over the southern half of Mexico; the third is known only from the state of Chiapas south to South America. No population estimates or trends are detectable through peer-reviewed literature. The three species are associated with primary tropical forests, both dry and wet (Ceballos and Oliva, 2005; Reid, 1997), and none is on the Mexican list of species at risk of extinction.

Three migratory bat species are considered threatened or endangered by the Mexican (SEMARNAT, 2002) and U.S. (U.S. Fish and Wildlife Service, 1988) federal governments. Conservation and recovery programs have been initiated and the bat populations are being monitored; surveys in recent years in several colonies suggest that the populations of at least two (*L. nivalis* and *L. curasoae*) of these three species in the genus *Leptonycteris* are stable. However, taking those species off the threatened or endangered species list may be premature. More local evidence is required before a firm conclusion can be drawn (Medellín, 2003; Medellín et al., 2004). Other pollinating bats might not be in decline, but those associated with primary habitats have long been considered rare, and their biology and importance are virtually unknown.

Nonflying Mammalian Pollinators

Among nonflying mammals, at least two species of opossum (*Caluromys derbianus* and *Didelphis marsupialis*; Tschapka and von Helversen, 1999) visit the flowers of *Marcgravia* in Central America. Coatis (*Nasua nasua*; Mora et al., 1999) and kinkajous (*Potos flavus*; Kays, 1999) have been documented as consistent flower visitors and potential or realized pollinators of various trees, including *Ochroma*, *Pseudobombax*, *Tetrathylacium*, and others. Janson et al. (1981) suggested that several primates (including the spider monkey, *Ateles*), opossums, and procyonids could be pollinators of several tree species in the rainforests, although at least the spider monkey has been shown to damage virtually all flowers it visits, apparently substantially decreasing fruit set (Riba-Hernandez and Stoner, 2005).

These mammals' habitats span southern Mexico to central Mexico and from the northern coatis range to southwestern United States. Opossums can also be found in southern Canada. The woolly opossum (*Caluromys derbianus*) is considered under special protection, and two of its subspecies are considered endangered. An endemic species of coati is threatened, and the kinkajou is under special protection (SEMARNAT, 2002). Pollination by nonflying mammals is reported more often for other continents (Carthew and Goldingay 1997; Goldingay et al. 1991).

Avian Pollinators

Pollination by birds is well known and recognized in North America, largely because of hummingbirds (Faegri and van der Pijl, 1966). Population data for avian pollinators are available from a variety of sources, including the North American Breeding Bird Survey (BBS) (see <http://www.mbr-pwrc.usgs.gov/bbs/genintro.html> for a history of this effort), which is now coordinated through the U.S. Geological Survey (USGS) Patuxent Wildlife Research Center. Bird banding data collected by individuals or at bird banding stations are compiled by the North American Bird Banding Laboratory, (<http://www.pwrc.usgs.gov/bbl/>) which also is part of the Patuxent Wildlife Research Center. Some summary BBS statistics are available from a USGS website (Sauer et al., 2005); some results are presented here. Cautious interpretation is necessary, however, because at least for hummingbirds, the BBS methodology is less than ideal.

Hummingbirds

Eighteen hummingbird species are known in the United States, 9 are known from Canada (although some of these are rare visitors from Mexico; Sibley, 2000), and 63 are known from Mexico. Most hummingbirds do not sing (even though they vocalize in aggressive interactions), so they can be more difficult to detect. Males and females can occupy different habitats, and males are polygynous—that is, they mate with more than one female in a breeding season.

Although a few species overwinter in the United States, most migrate southward, depending on migration corridors or nectar corridors (Nabhan et al., 2004). It can be difficult to assess hummingbird populations because some surveys (such as the Christmas Bird Counts) are conducted when individuals might have left for wintering grounds. There is evidence that a high percentage of rufous hummingbirds (*Selasphorus rufus*) lose body weight during migration, requiring longer stopover times if floral resources are scarce (Russell et al., 1994).

The relationship between hummingbirds and the flowers they visit

is well studied (Arizmendi and Ornelas, 1990; Calder, 2004; Grant and Grant, 1967), and hummingbirds are important pollinators in much of North America. Although hummingbirds visit a wide variety of flowers, many hummingbird-pollinated flowers share some general characteristics. The flowers tend to be tubular, brightly colored (red, orange, bright yellow), and relatively odorless, and their nectar is often more diluted than that of bee-pollinated flowers (Baker, 1975; Pyke and Waser, 1981) but could contain higher levels of sucrose (Baker et al., 1998). Hummingbirds display variation in bill shape and length (Stiles and Skutch, 1989), and some studies indicate that all hummingbirds can extract nectar from long-tubed, wide-opening flowers, but that only long-billed hummingbirds do so from long-tubed, narrow-opening flowers (Temeles et al., 2002). The list of species of plants that are visited and pollinated by hummingbirds is extensive (Bertin, 1982; Grant and Grant, 1968), and it encompasses plants in many families: Acanthaceae, Asteraceae, Bromeliaceae, Campanulaceae, Ericaceae, Fabaceae, Gentianaceae, Heliconiaceae, Loranthaceae, Malvaceae, Onagraceae, Polemoniaceae, Rubiaceae, Zingiberaceae, and many others (Knudsen et al., 2004; McDade and Weeks, 2004).

Although hummingbirds might be minor as pollinators of agricultural crops (cacti; Griffith, 2004), many species of wildflowers have coevolved with hummingbirds and exhibit morphological, phenological, or other traits that facilitate interaction (Fenster et al., 2004). Data from BBS with a high credibility index (at least 14 samples in the long term, of moderate precision, and of moderate abundance on routes) are available for 8 hummingbird species. Data cited below come from the BBS website (<http://www.mbr-pwrc.usgs.gov/bbs/bbs.html>).

In the states where the credibility index is high (such as North Carolina, Oklahoma, and West Virginia), the trend (percentage change per year) shown for the ruby-throated hummingbird (*Archilochus colubris*) from 1966 to 2005 is positive. Overall, trends in the United States (2.5 percent per year) and Canada (2.5 percent per year) are positive (<http://www.mbr-pwrc.usgs.gov/cgi-bin/atlas99.pl?04280&1&05>). For the black-chinned hummingbird (*Archilochus alexandri*), for one site (Edward's Plateau) for which the credibility index is high, the trend from 1966 to 2005 is positive (1.2 percent per year). Overall, the trend for *A. alexandri* is positive in the United States (1.6 percent per year), and negative in Canada (−3.2 percent per year). For Anna's hummingbird (*Calypte anna*), in the states where the credibility index is high, the trend from 1966 to 2005 is positive; the data set includes California, a state with a few regions—California, Southern California grasslands, foothills, and Fish and Wildlife Service Region 1. Overall, the trend is positive (1.2 percent per year) in the United States. For the broad-tailed hummingbird (*Selasphorus platycercus*), in the states where the credibility index is high, the trend from 1966 to 2005 is mixed;

it is slightly negative in Colorado and slightly positive in New Mexico. Overall, the trend is slightly negative (−0.2 percent per year) in the United States. Calder et al. (1983) reported that, over a 10-year period at the Rocky Mountain Biological Laboratory, the population of *S. platycercus* appeared to be declining, although nest counts of breeding females remained fairly constant. In the years since that study, the population has remained variable, but with no discernable long-term trend (D. Inouye, University of Maryland, and Rocky Mountain Biological Laboratory, Colorado, personal observation). For the rufous hummingbird (*Selasphorus rufus*), in Oregon and Washington, the two states where the credibility index is high, the trend from 1966 to 2005 is negative. Overall, trends in the United States (−2.0 percent per year) and Canada (−2.1 percent per year) are negative. An interesting development over the past decade is that rufous hummingbirds are commonly found in the eastern United States, where they previously were thought to be absent.

The status of several species, because of a lack of information, is more difficult to determine. For the Costa hummingbird (*Calypte costae*), there are no states where the credibility index is high, but the trend from 1966 to 2005 is positive for one state with a few regions—the Great Basin deserts and Mexican highlands. Overall, the trend is positive (0.5 percent per year) in the United States. Similarly, for the calliope hummingbird (*Stellula calliope*), there are no states where the credibility index is high, but the trend from 1966 to 2005 is positive in Idaho and Wyoming and negative in California, Montana, Oregon, and Washington. Overall, the trend is negative (−0.9 percent per year) for the United States and slightly positive (0.8 percent per year) for Canada. There is no statistically significant detectable trend. Finally, for the Allen hummingbird (*Selasphorus sasin*) there are no states with a high credibility index, but in the southern Pacific rainforest region—the only region with a high index—the trend from 1966 to 2005 is negative (−1.2 percent per year) but edging upward over the past several years. Overall, the trend for *S. sasin* in the United States is negative (−2.0 percent per year). This species is on the Audubon Society Watch List because of its very restricted range in the United States. There are two subspecies, identified primarily through their distribution (mainland or the Channel Islands off the coast of Southern California), and although the subspecies with the wider range (coastal Mexico to Oregon) appears to be in decline, the other appears to be spreading.

Unfortunately, there do not appear to be any long-term data about population trends of species of hummingbirds that are distributed in Mexico exclusively. Although these species could be under pressure from habitat alteration and fragmentation, there is no equivalent of the BBS data and no systematic banding efforts that the committee could discover.

Nonhummingbird Avian Pollinators

Although not typically thought of as pollinators, at least one dove species, the white-winged dove (*Zenaida asiatica*), is an important pollinator of saguaro and possibly other cacti (Fleming, 2000). The population trend for that species is slightly negative from 1966 to 2005 in Arizona, the Sonoran Desert, and the Mexican highlands. Overall, in the United States and in the survey area, the trend is positive (1.6 percent per year). A few other nonhummingbird avian species also pollinate North American plants, and there is evidence that they also affect flower morphology. The genus *Erythrina* (Fabaceae), a pantropical leguminous small tree, shows two distinct flower and nectar types: hummingbird-pollinated species have upright inflorescences with tubular, radially arranged flowers and nectar that has relatively high concentrations of sugar. The species pollinated by passerine birds (including swallows) have horizontal inflorescences held upright, with the flowers arranged radially along the axis, the narrow standard petal folded to form a pseudotube, and relatively dilute nectar (Bruneau, 1997). Several species have been identified: verdins (pollinating ocotillo, *Fouquieria splendens*; Waser, 1979), oriole (*Icterus* spp.: Etcheverry and Aleman, 2005; Toledo and Hernandez, 1979), parrot (*Aratinga*), woodpecker (*Centurus*), tityra (*Tityra*), warbler (*Dendroica*), wren (*Campylorhynchus*), jay (*Psilorhynchus*), vireo (*Vireo*), blackbird (*Dives*), grackle (*Cassidix*), oropendola (*Psarocolius*), honeycreeper (*Cyanerpes*), tanager (*Thraupis*, *Piranga*), euphonia (*Euphonia*), mockingbird (*Mimus*), thrasher (*Toxostoma*), and finch (*Carpodacus*) visit flowers of a diverse array of species including *Bernoullia*, *Ceiba*, *Tabebuia*, *Spathodea*, and *Agave* (Ornelas et al., 2002; Toledo, 1977).

Some bird species of these genera are on the Mexican federal list of endangered species: six vireo species are under special protection, two species are threatened, and one is endangered. Three orioles and two oropendolas are under special protection; two parrots of the genus *Aratinga* are under special protection, two more are threatened, and one subspecies of one threatened species is considered endangered. Two species of warbler are threatened, and one wren species is under special protection, one is threatened, and one is endangered. Two euphonias are under special protection, one thrasher is endangered, and two subspecies of finch are endangered (SEMARNAT, 2002).

Information Needs

As the number of individual hummingbird banders in the United States has grown, so has the amount of information about the birds' abundance and migration paths. Additional data might have been collected at some

long-term bird banding stations or by long-term individual banders that could add to the incomplete data for hummingbirds. Long-term monitoring of bird-pollinated plants also could provide useful information on the stability of the ecosystem services they provide, particularly if plants pollinated solely by the birds are chosen.

CONCLUSIONS

Despite the paucity of long-term data, collectively there is reliable evidence that some North American pollinator species have become extinct or locally extirpated, or have exhibited decreases in population size (Table 2-6). At least two bumble bee species could face imminent extinction, and several other pollinators have declined significantly (honey bees and U.S. and Mexi-

TABLE 2-6 Illustrative Examples of Pollinators in North America for Which Evidence of Decline Is Available

Common Name	Species Name	Location
<i>Species for Which Quantitative Data Are Available</i>		
	Hymenoptera	
Honey bee	<i>Apis mellifera</i>	United States
Honey bee	<i>A. mellifera</i>	Mexico
Franklin's bumble bee	<i>Bombus franklini</i>	Pacific Northwest of the United States
Western bumble bee	<i>B. occidentalis</i>	Central California
Bumble bee	<i>B. affinis</i>	New York
	Lepidoptera	
Bay checkerspot butterfly	<i>Euphydryas editha bayensis</i>	Palo Alto, California and other localities
	Chiroptera	
Long-nosed bat	<i>Leptonycteris curasoae</i>	United States and Mexico
Long-nosed bat	<i>L. nivalis</i>	United States and Mexico
	Apodiformes	
Rufous hummingbird	<i>Selasphorus rufus</i>	United States and Canada
Allen's hummingbird	<i>S. sasin</i>	United States
<i>Species for Which Quantitative Data Are Not Available</i>		
	Hymenoptera	
Stingless bees	<i>Melipona</i> spp.	Southern Mexico
	<i>Trigona</i> spp.	
Pollen wasps	<i>Pseudomasaris micheneri</i>	Inyo County, California
Pollen wasps	<i>P. macswaini</i>	
	Chiroptera	
Hog-nosed bat	<i>Choeronycteris mexicana</i>	Mexico
Banana bat	<i>Musonycteris harrisoni</i>	Mexico

can pollinating bats), although many have populations that are stable or perhaps even increasing, as are a few of the hummingbird species. It should be noted that there is no evidence of population decline for some species merely because their populations have not been monitored over time. Overall, whether there is a “pollinator crisis” is difficult to ascertain inasmuch as there is no definition of “crisis” that is universally accepted; however, if “decline” is defined as a systematic decrease in population size over time, then there is evidence that some pollinators in North America representing a diversity of taxa are, in fact, in decline. It is accordingly important to ascertain the causes and the consequences of those declines as a step toward informed decision making about action to be taken and what would most likely ensure successful reversal.

3

Causes of Pollinator Declines and Potential Threats

It is difficult to determine whether North American pollinator species are declining, and no less challenging is determining the causes of putative declines or local extirpations. Many explanations have been invoked to account for declines in pollinator populations in North America, including, among others, exposure to pathogens, parasites, and pesticides; habitat fragmentation and loss; climate change; market forces; intra- and inter-specific competition with native and invasive species; and genetic alterations. Careful evaluation of the literature allows some causes to be assigned, but explanations are ambiguous or elusive for other species losses.

DECLINE IN ACTIVELY MANAGED POLLINATORS

Honey Bees (*Apis mellifera* L.)

The best evidence of specific pollinator decline is seen in the western honey bee, *Apis mellifera* L., the primary commercial pollinator of agricultural crops in North America and the most widely used, actively managed pollinator in the world (Delaplane and Mayer, 2000; Kearnes et al., 1998; McGregor, 1976). The population losses among honey bees are elucidated in a large body of literature on honey bee pests, parasites, and pathogens (Morse and Flottum, 1997), most notably on the parasitic mites *Varroa destructor* (varroa mite) and *Acarapis woodi* Rennie (tracheal mite), the pathogen *Paenibacillus larvae* (American foulbrood, [AFB]), and the invasive Africanized honey bee.

Parasitic Mites

Varroa Mite (*Varroa destructor*)

The supply of healthy and affordable honey bee colonies for crop pollination clearly has been threatened by the arrival of parasitic mites *Varroa destructor* and *Acarapis woodi*. Since 1981—just before the arrival of *A. woodi*—stocks of honey bee colonies in the United States have declined by 39 percent (Figure 2-1; USDA-NASS, 1995, 1999, 2005, 2006). Parasitism by mites of honey bees is a relatively recent problem in North America. A 1980–1982 survey of samples from 4,400 apiaries in the United States and Canada revealed no evidence of mite infestation (Shimanuki et al., 1983). The varroa mite was first reported in the United States in 1987 (Anonymous, 1987) and within a decade it had become established throughout the United States.

Varroa destructor (Anderson and Trueman, 2000) has caused dramatic declines in honey bee abundance in North America and throughout the world (DeJong, 1990; DeJong et al., 1982a; Sammataro et al., 2000). The varroa mite is an obligate external parasite of *A. mellifera* and *Apis cerana* (eastern honey bee) that was first described as *V. jacobsoni* (Oudemans, 1904) in Java. It exists there in a stable and sustainable association with *A. cerana*, its native host (Rath, 1999). In eastern honey bee colonies, female varroa mites reproduce almost exclusively on male (drone) larvae or pupae (Koeniger et al., 1983), so they do not affect the population size of the female worker force. The biology of *A. cerana*, including its relationship with the varroa mite, is discussed by Kevan et al. (1996) and by Oldroyd and Wongsiri (2006).

The association of *V. destructor* with the western honey bee, *A. mellifera*, reportedly began in the 1950s (Matheson, 1995) when the mites moved into honey bee colonies brought into the home range of *A. cerana*. Subsequently, the varroa mite has established a nearly cosmopolitan distribution with respect to its new host, and Australia is now the only mite-free continent (Matheson, 1995). It is not known how this parasite entered the United States.

In *A. mellifera*, female varroa mites reproduce on both worker and male larvae. Infestation of honey bee colonies of European origin (the source of most *A. mellifera* introduced to North America) is fatal if untreated, and colony mortality usually occurs 6 months to 2 years after the initial infestation (DeJong, 1990).

Newly emerged adult worker bees parasitized as pupae exhibit a range of symptoms: substantial loss of adult weight (DeJong et al., 1982a,b; Engels and Schatton, 1986), reduced concentrations of serum proteins (Engels and Schatton, 1986), impaired development of (brood food-producing) hypopharyngeal glands (Schneider and Drescher, 1987), severe deformations of

the wings (Akratanakul and Burgett, 1975), and reduced longevity (DeJong and DeJong, 1983).

Varroa parasitism of *A. mellifera* drones also can affect the ability of the queen to obtain adequate supplies of healthy sperm during mating. Parasitism has been associated with reduced sperm quality (Collins and Pettis, 2001) and with decreases in adult weight, size of seminal vesicles, and mucus. Effects of parasitism on male behavior include a decline in the frequency of flight (Schneider, 1986) and decreased flight performance, sperm production, and mating efficiency (Bubalo et al., 2005; Duay et al., 2002).

Varroa parasitism of honey bees is associated with viral pathogens, and some damage attributed to varroa mites is actually viral in origin (Allen and Ball, 1996). Although some viral diseases of honey bees are associated with varroa infestations (Kevan et al., 2006; Oldroyd and Wongsiri, 2006), which negative effects are exclusively attributable to direct actions of the mites or to their associated pathogens is unknown (Chen et al., 2005). “Parasitic mite syndrome” is used to describe colonies that exhibit a constellation of symptoms, including the presence of diseased adult and immature bees, adults with deformed wings, and crawling bees at hive entrances (Shimanuki et al., 1994). Once this syndrome is apparent, the colony begins a rapid decline in adult worker population and viable replacement brood. It dies, typically within 3–6 weeks of the onset of symptoms.

The rate at which the varroa mite population increases in a honey bee colony depends in part on the rate at which individual mites reproduce (Fries et al., 1994). Some stocks of honey bees, such as neotropical Africanized honey bees (see section on Invasive Species in this chapter), are less susceptible to varroa mites than are other stocks, apparently because they have slightly faster developmental times, thus depriving the mites of the time necessary for successful reproduction (Camazine, 1986).

Twenty years after its introduction to the United States, *V. destructor* continues to devastate honey bee populations. High losses have been reported locally (Burgett, 1994; Loper, 1995) and nationally. During the winter of 1995–1996, northern U.S. beekeepers experienced their largest losses in history; in some states, 30 to 80 percent of colonies were lost (Finley et al., 1996). Similar losses were observed in the winters of 2000–2001 and 2004–2005 (Caron and Hubner, 2001; Lumkin, 2005). Data on colony losses are derived from informal surveys of beekeepers, and the exact causes of colony deaths have not been established. However, except for the large loss of honey bee colonies in the 1940s from the bacterial disease, AFB, losses on this scale were never reported before the detection of parasitic mites (Finley et al., 1996). These honey bee losses have occurred despite the industry’s heavy reliance on pesticides to control mite populations. Pesticide resistance has become widespread (Elzen et al., 1998, 1999d) and many beekeepers are no longer able to use the few registered pesticides for varroa control.

New miticides formulated from natural products (Calderone, 2000; Calderone and Nasr, 1999; Calderone and Spivak, 1995; Calderone et al., 1997) and fungal pathogens *Hirsutella thompsonii* and *Metarhizium anisopliae* have shown promise, but problems with temperature sensitivity and treatment methods remain unresolved (Kanga et al., 2003a,b).

Operating costs for beekeepers have increased because of varroa mite infestations (Kemp, 2000); expenses include those for pesticide treatment (material and labor) and to replace colonies killed by the mites. Replacing colonies also requires additional labor and, because the new colonies are smaller, they produce less honey the first year than healthy colonies that have successfully wintered (Morse, 1994). The bee industry badly needs improved methods for managing varroa mites, including methods of breeding for resistance in hosts (Chapter 6).

Tracheal Mite (Acarapis woodi)

The tracheal mite *Acarapis woodi* is an internal parasite of *A. mellifera*. Initially identified in the United Kingdom in 1921 (Imms, 1921; Rennie, 1921), tracheal mites were first detected in the United States in 1984 in Texas, where they most likely entered into the country on swarms of bees from Mexico (Eischen et al., 1990; Hall and Eischen, 1991; Pettis et al., 1987). At first, tracheal mites caused serious damage to colonies in the United States (Eischen, 1987; Eischen et al., 1989; Frazier et al., 1994; Otis, 1990; Sammataro et al., 2000; Scott-Dupree and Otis, 1991), but attention to tracheal mites has diminished as beekeepers struggle to manage the more problematic varroa mite. Perhaps this is also related to findings of heritable variation in honey bees for resistance to tracheal mites (Gary et al., 1990; Nasr et al., 2001; Page and Gary, 1990). Several chemical treatments have been identified to control tracheal mites (Calderone and Shimanuki, 1995; Clark, 1990; Delaplane, 1992; Wilson and Collins, 1993; Wilson et al., 1989, 1990). The current status of the tracheal mite and its impact on honey bees are unknown.

Pathogens

Paenibacillus larvae (formerly *Bacillus larvae*: White, 1920) is the most serious honey bee pathogen. It causes AFB, a disease of larval honey bees. AFB is highly virulent and easily spread among colonies as a result of beekeeper activity and bee behavior, and it is generally fatal if untreated (Shimanuki, 1997). During the first half of the 20th century, AFB was the most serious threat to beekeeping, and it caused tremendous loss of colonies, amounting to hundreds of thousands in the 1940s (Barrett, 1955). The incidence of AFB was reduced dramatically by the introduction of antibiotics

and by state apiary inspection programs that required the burning of infected hives (Barrett, 1955).

Sulfathiazole (Hasemans and Childers, 1944) was the first effective chemotherapeutic agent used to control AFB, but its use was discontinued in the United States because of concerns with residues in honey (Lodesani and Costa, 2005). Gochnauer (1951) reported good control with oxytetracycline (Terramycin®) and was a mainstay in AFB prevention until the 1990s (Wilson, 1970; Wilson et al., 1973). However, AFB is troublesome because its spores are refractory to antibiotics (Shimanuki, 1997) and can persist on contaminated equipment for more than 80 years. Treatment of colonies with active cases of AFB eliminates disease symptoms, but withdrawal of antibiotics is generally followed by disease recurrence (Allipi et al., 1999).

Even when infected colonies are treated with antibiotics, there is still a major threat to nearby healthy colonies because the infected colonies can serve as reservoirs of infective spores. Consequently, the use of oxytetracycline is recommended as a preventive rather than as a treatment for active cases. Most states still require that colonies with active cases of AFB be destroyed and the equipment be burned or buried (Ratnieks, 1992).

Resistance to the antibiotics used against AFB was not observed in the United States until about 1994 (Shimanuki and Knox, 1994), but it has become widespread, and AFB is now a resurgent threat to the industry (Cox et al., 2005; Evans, 2003). Tylosin tartrate (Tylan®) is an effective control agent (Alippi et al., 1999; Elzen et al., 2002; Hitchcock et al., 1970) that recently received Food and Drug Administration approval (FDA-CVM Update, October 20, 2005). However, a single chemical treatment is only a short-term solution, as has demonstrably been the case with treatment for varroa mites.

Pesticides

The application of pesticides, especially insecticides used to control crop pests, kills or weakens thousands of honey bee colonies in the United States each year (Johansen and Mayer, 1990). Local bee kills have occurred sporadically for decades and likely have not contributed significantly to the recent national decline in colony populations (Chapter 2). Most pesticide-caused bee kills are the result of accidents, careless application, or failure to adhere to label recommendations and warnings (Johansen and Mayer, 1990).

A few examples illustrate the nature of the problem: mosquito control programs have resulted in major losses of honey bees in Canada and the United States (Dixon and Fingler, 1982, 1984). In Manitoba, efforts to combat serious outbreaks of western equine encephalitis by controlling its mosquito vectors resulted in colony losses that amounted to \$850,000 in

1983 (Dixon and Fingler, 1984). In California, between 1966 and 1979, before the emergence of the varroa mite, insecticides caused the death of more than 1 million colonies—accounting for 47 percent of bee colony deaths in that period—causing a 10 percent decrease in population (NRCC, 1981, Table 6, p. 83).

Recent trends in North America and many other parts of the world are toward reducing the use of pesticides in agriculture and forestry, to mitigate problems associated with pesticide applications, and adopting such practices as restricting spraying to times when pollinators are not foraging (Adey et al., 1986; Johansen and Mayer, 1990). In a lawsuit against the State of Minnesota and the International Paper Company (the landowners), beekeepers alleged that the landowners sprayed carbaryl insecticide (Sevin XLR Plus) to control cottonwood leaf beetles (*Chrysomela scripta*) despite the knowledge that the tree plantations were within the foraging range of beekeepers' apiaries. Although the case was disposed by the Minnesota District Court, the Supreme Court reversed the District Court's decision (http://www.beyondpesticides.org/news/daily_news_archive/2005/03_10_05.htm). The State of Minnesota settled out of court with a \$335,000 payment to beekeepers (Anonymous, 2005; Schell, 2005).

Sublethal effects of pesticides on bee foraging behavior have been reported (Pham-Delegue et al., 2002). For example, there have been reports in Europe that exposure to Gaucho® (imidacloprid) impairs the navigational and foraging abilities of honey bees. These results have not been obtained in all studies (Pham-Delegue et al., 2002), and the effect of imidacloprid on honey bees is controversial. However, other pesticides have been shown to impair bee behavior, so the threat of sublethal effects of pesticides on bee foraging behavior is real.

The negative impact of pesticides on managed honey bee colonies suggests that feral bee populations could be similarly affected by pesticides, but there are no studies on the latter subject to the committee's knowledge. Feral honey bees have not been studied intensively (see Chapter 2). Pesticides can potentially harm many bee species and even eliminate some pollinator populations in ecosystems. However, bee populations seem to recover once pesticide application ceases (for example, Kevan et al., 1997) unless the populations are eliminated over a very large area.

Transgenic Crops

Transgenic crops were developed in part to reduce the unintended effects of pesticides. However, the deployment of crop plants genetically engineered to express insecticidal proteins in pollen raised questions about direct effects on nontarget species, including some pollinators (Losey et al., 1999). For honey bees, the concerns involved the potential lethality of insecticidal

transgenic proteins, the sublethal effects of these proteins on insect behavior, physiology, and reproduction and the economic effects of transgenic pollen as a contaminant of honey. Malone and Pham-Delègue (2001) reviewed the small literature on this topic and concluded that, in some cases, there are negative but sublethal effects attributable to consumption of transgenic pollens. These effects varied with the identity of the transgene and the amount of its expression but in no case have any effects of transgenic crops on honey bee populations been documented.

Invasive Species

Africanized Honey Bees

The Africanized honey bee is a hybrid of the African race, *A. mellifera scutellata*, intentionally introduced to Brazil in the early 1950s (Winston, 1992), and European races of *A. mellifera* introduced with European colonists in the 1600s (Sheppard, 1989a,b). The Africanized honey bee gained some measure of notoriety because it is more defensive than most European races of honey bee; when disturbed, colonies of Africanized honey bees respond more aggressively and with more rapid and prolonged stinging behavior (Winston, 1992). The spread of the Africanized honey bee from South to North America is one of history's most spectacular examples of biological invasion (Roubik, 1989; Schneider et al., 2004). Several traits have facilitated the establishment of Africanized honey bees: their colonies grow faster than do those of the European honey bees, and there are genetic incompatibilities in hybrids that favor loss of European traits; African drones exhibit mating advantages; Africanized bees have a greater ability to establish nests in a broader variety of locations; and they exhibit more nest usurpation behavior than do European bees (Schneider et al., 2004). The influx of Africanized bees into the United States began several years after resident honey bee populations had experienced sharp declines (Chapter 2); Africanization of U.S. bees was not a cause of those declines.

Africanized honey bees were first detected in the United States in Hidalgo, Texas, in 1990 (Hunter et al., 1993). They have spread throughout the Southwest, parts of California, and most recently (National Plant Board, 2005), parts of the Southeast including Florida (Figure 3-1). Africanized honey bees have not spread into Canada because the border between the two countries has been closed to transport of honey bees since tracheal mites were detected in the United States (see Chapter 2). If the border were to reopen to allow imports of packaged bees and queens from the United States, there would be potential for Africanized bees to be imported to Canada.

Although the Brazilian (DeJong, 1996; Goncalves et al., 1991) and Mexican (Guzman-Novoa and Page, 1994a, 1999) bee industries eventually

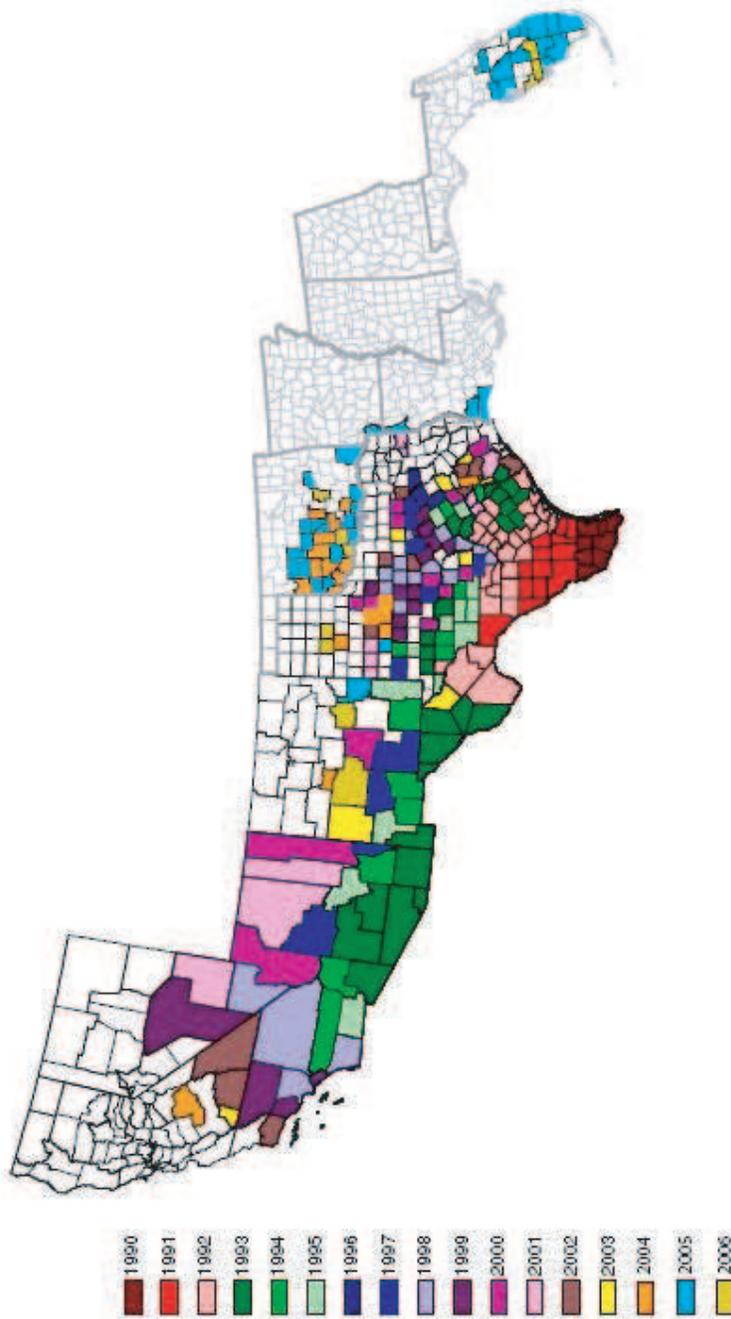


FIGURE 3-1 Current distribution of Africanized honey bees. SOURCE: USDA-ARS.

have adjusted well to Africanized honey bees, beekeeping in Mexico and Brazil differs in many fundamental ways from that in the United States and Canada, and experiences with Africanized bees in those countries might not serve as useful models for the rest of the hemisphere.

The presence of Africanized bees throughout the southern and southeastern United States could exacerbate losses of European honey bee colonies documented in Chapter 2 (Winston, 1992). Africanized bees reproduce (“swarm”) more often than do European bees (Danka and Rinderer, 1986; Winston, 1979; Winston et al., 1981), which has two important consequences. First, colonies are weakened as a result, and weaker colonies do not pollinate as efficiently as stronger colonies (Winston, 1987). Second, swarms of honey bees often settle in places near humans, posing an increased health hazard.

Colonization by Africanized honey bees might make it more difficult to obtain replacement queens and packages from desirable stocks. As Africanized honey bees move northward, farther into California, and eastward into the southeastern United States, they will enter the principal queen- and package-producing regions (northern California, Georgia, Alabama, Louisiana, Mississippi, Florida) and wintering areas for migratory beekeepers (Florida, Louisiana, South Carolina, Texas), who move their colonies as crops come into bloom. Each year, the bee packaging industry supplies at least a million queens and packages of bees (Schiff and Sheppard, 1995, 1996) for replacement of colonies that succumb to winter stress, mites, or the rigors of migratory beekeeping. About half of the queens are produced in the western United States and half in the southeastern United States.

Africanized honey bees will also encroach on prime agricultural regions such as the almond orchards in California. Africanized honey bees are less desirable than European honey bees as commercial pollinators because they forage over relatively short distances (Danka et al., 1993) so they are not appropriate for some crops. They also are more likely to abandon their colonies altogether when food is scarce (Danka et al., 1987; Winston et al., 1979, 1983), and shortages of nectar can occur when honey bee colonies are used at high densities to pollinate orchards or fields. Most important, Africanized honey bees’ aggressive behavior contributes to increased liability costs and regulations banning the movement of bees into or through certain areas (Danka et al., 1987). Beekeepers are almost entirely dependent on the goodwill of rural property owners to find locations for their apiaries.

Predictions about the eventual distribution of Africanized honey bees in the United States vary. Some researchers suggest Africanized bees will become established across all the southern states (Dietz and Vergara, 1995; Rinderer, 1986; Taylor, 1977). Africanized bees are not likely to survive in the interior portions of the United States, but partially Africanized colonies (European or Africanized queens mated to one or more Africanized drones)

could (Dietz and Vergara, 1995). The seasonal movement of packages, queens, and beekeepers servicing crops both within and outside areas with Africanized honey bees could contribute to an increase in range, even if temporary in some locales.

Small Hive Beetle (*Aethina tumida*)

Native to South Africa (Lundie, 1940), the small hive beetle (*Aethina tumida*) was detected in the United States in 1998 (Thomas, 1998), but how it arrived is not known. Adults and larvae eat pollen, honey, and brood, in the process damaging colonies and beekeeping equipment (Thomas, 1998). They especially damage combs of unextracted honey stored in honey houses (Hood, 2004a); the larvae burrow through the combs and defecate in them, causing the honey to ferment and leak from the combs (Headings, 2000).

The small hive beetle is found throughout the eastern United States, although it is considered an economically important pest only along the southeastern coast (Hood, 2004b). In northern states, it is a manageable pest of honey houses that is not associated with colony losses (Neumann and Elzen, 2004). Whether it becomes a more noxious pest could depend on its capacity to expand its range; its ultimate distribution in the United States could be affected partly by soil conditions (Ellis et al., 2004a). Whether it will remain manageable is an open question as well. Chemical controls are available (Elzen et al., 1999b), and biological control agents show promise (Ellis et al., 2004b; Richards et al., 2005). Racial variation in the response of honey bees to *A. tumida* infestation (Elzen et al., 2001) suggests that selection for resistance to this pest, like selection for resistance to AFB and varroa mites, is possible.

Bumble Bees (*Bombus* spp.)

Starting in the early 1990s, companies in Europe (Banda and Paxton 1991), Israel, and Canada (Kevan et al., 1991) developed commercial insectary techniques for mass-rearing bumble bees year-round to pollinate tomatoes, sweet peppers, and several other greenhouse crops (Banda and Paxton, 1991; Kevan et al., 1991). In the United States and Canada, *Bombus impatiens* and *B. occidentalis* have been the main species used commercially, although *B. occidentalis* has not been reared by Koppert since 1998 (M. Tacolla, Koppert Biological Systems, Inc., personal communication, March 2006), and the other company is closing its rearing program soon (R. Ward, Biobest Canada Ltd., personal communication, June 2006). Because bumble bees are reared and deployed for pollination at high densities—as many as 23,000 individuals per greenhouse (Morandin et al., 2001)—they are particularly vulnerable to pathogens and parasites.

Parasites

Bumble bees suffer from infestation by several parasites, notably the protozoans *Nosema bombi* and *Crithidia bombi* and the tracheal mite *Locustacris buchneri* (Imhoof and Schmid-Hempel, 1999; Shykoff and Schmid-Hempel, 1991). The two protozoan parasites often occur together in European bumble bees. Although *C. bombi* is suggested not to be native to North America (its natural host is the European *B. terrestris*), it has been found in *B. impatiens* and *B. occidentalis* in North America, likely because the three species were reared together in the same insectary facilities in Europe (Colla et al., 2006; Thorp, 2003; Winter et al., 2006) during the years when queens collected in North America were sent to Europe to establish colonies and then returned to North America. Presumably, cross-infected bees returned to North America for pollination of greenhouse crops also foraged outside the greenhouses and infected wild bees (Colla et al., 2006).

A new threat to bumble bees is deformed wing virus, originally a disease of honey bees, that has been found in *B. terrestris* in European commercial breeding operations and in a feral colony of *B. pascuorum* in Germany (Genersch et al., 2006). The frequency of this disease in honey bees is increasing because of oral transmission and transmission by varroa mites; in bumble bees, transmission appears to be exclusively oral. Discovery of this virus in bumble bees raises questions about transmission and cross-infectivity among bumble bees and between bumble bees and honey bees, as well as the potential risks of commercial trafficking in bumble bees (R. Thorp, University of California, Davis, personal communication, April 2006).

There is growing evidence of the proliferation of exotic pathogens and parasites in populations of commercially reared bumble bees in the United States and Canada (Colla et al., 2006). Bumble bees used in greenhouse pollination frequently harbor high levels of different pathogens (Colla et al., 2006), and infected colonies exhibit reduced survival and reproduction and diminished foraging efficiency (Brown et al., 2003; Fisher and Pomeroy, 1989; Gegear et al., 2005; Husband and Sinha, 1970; Macfarlane et al., 1995; Otterstatter et al., 2005). *Nosema bombi* is globally associated with bumble bees, and its ubiquity in managed colonies presents a palpable risk to wild bumble bee populations in North America (Flanders et al., 2003; Thorp et al., 2003).

Pesticides

The damage to honey bees inflicted by insecticides suggests that similar problems occur for other managed and unmanaged bee species (Helson et al., 1994; Johansen and Mayer, 1990; Torchio, 1973). Nontarget effects, however, particularly in unmanaged populations, tend to be poorly documented,

so the scope of the problem is unclear. The few comparative studies give evidence that pesticide toxicities are not necessarily predictive of the hazards to other bee species (Johansen and Mayer, 1990; Kevan and Plowright, 1995; NRCC, 1981). Like honey bees, bumble bees can be exposed to pesticides while foraging (Gels et al., 2002; Tasei et al., 2001). Ground-nesting bumble bees, however, are uniquely susceptible to pesticides applied to turf or lawns for grub control (Gels et al., 2002). Effects can be sublethal (Belzunces et al., 2001; Tasei et al., 1994); for example, imidacloprid (Morandin et al., 2005) and clothianidin (Franklin et al., 2004) can hamper foraging and pollinating. Morandin and Winston (2003), however, reported no effects of the transgenic (insecticidal) proteins Cry1ac or chitinase.

Because almost all bumble bee deaths caused by pesticide exposure are unreported, determining their implications for bumble bee population declines is difficult, if not impossible. Thompson (2001) suggested that non-target exposures can disproportionately affect bumble bee numbers if they occur early in the season when queens are still foraging and when colonies are very small (Thompson, 2001). During studies on the environmental effects of fenitrothion on pollination and bumble bees in New Brunswick, Canada, Plowright and his colleagues (1978) noted severe bumble bee population reductions that were evidenced in changed foraging behavior of surviving colonies. Foraging trip times declined because there was less competition with congeners for floral resources and the bumble bee populations rebounded quickly (reviewed in Kevan and Plowright, 1995).

Alfalfa Leafcutting Bees (*Megachile rotundata* F.)

Alfalfa (= lucerne) is a major forage crop grown for free-ranging livestock and as hay for livestock feed. In the United States, about 25 million acres (about 10 million hectares) of alfalfa are planted annually, and the crop has an estimated value of more than \$5 billion (Flanders and Radcliff, 2000). The primary pollinator is the introduced alfalfa leafcutting bee *Megachile rotundata* F. Management techniques for this solitary bee are well developed (Peterson et al., 1992; Stephen, 2003); however, chalkbrood disease nearly destroyed the production of leafcutting bees in the United States.

Chalkbrood is a fungal disease caused by *Ascospaera aggregata* Skou (Goettel et al., 1997; Vandenberg and Stephen, 1983). Larvae contract chalkbrood by ingesting pollen contaminated with fungal spores. After germinating in the midgut, the fungus infiltrates the hemocoel and mycelia proliferate, turning the body chalk-white (Vandenberg and Stephen, 1983). The disease was first noted in Nevada in 1973 and has since spread to most areas in western North America (Stephen et al., 1981), where total bee mortality rates can exceed 60 percent.

Because chalkbrood disease is less common in Canada, most leafcutting

bee production in North America is in British Columbia, Saskatchewan, Alberta, and Manitoba. Although some seed growers in the United States can replace bee stocks in a good year, a loss of 50 percent or more is typical. Consequently, large numbers of alfalfa leafcutting bees are imported from Canada each year (R. Bitner's presentation to the committee, January 14, 2006). Canadian beekeepers produce large numbers of healthy bees, perhaps because of increased resistance to chalkbrood in Canadian stocks (Vandenberg, 1991). But if chalkbrood disease becomes endemic in Canada, leafcutting bee production could be jeopardized (Peterson et al., 1992). Efforts to select for resistant stocks of *M. rotundata* in the United States have been unsuccessful (Stephen and Fichter, 1990a,b). Although recent records are difficult to find, there have been losses of alfalfa leafcutting bees caused by pesticides in the western United States (Johansen, 1977). In Manitoba, law protects alfalfa leafcutting bees from pesticide applications (Tang et al., 2005).

Alkali Bee (*Nomia melanderi* Cockerell)

The alkali bee, *Nomia melanderi* Cockerell, is the world's only intensively managed ground-nesting bee. In regions of the western United States, particularly in southeastern Washington and formerly in several other areas (among them, Lovelock, Nevada), alfalfa seed growers construct large sub-irrigated nest sites with salt-crusted surfaces for this bee. Densities of 400 nests per square meter over a hectare or more can be obtained with this gregarious bee (Bohart, 1970, 1972a; Fronk, 1963).

Alkali bee mortality can be caused by a variety of vertebrate and invertebrate predators, microbial pathogens, inadvertent pesticide exposure (especially aerial applications of pesticide for rangeland grasshoppers), vehicular traffic (which can kill bees crossing roads near their nest sites), and nest site flooding. Economic factors, however, were primarily responsible for declines in North American populations. Low prices for alfalfa leafcutting bees led growers to abandon the maintenance of nesting sites, leading to a decrease from peak populations of more than 400,000 nesting females per site to a few thousand per site in Touchet Valley, Washington. Prices of leafcutting bees have risen recently, as have prices of alfalfa, leading to an increase in the cultivation of alkali bees (Stephen, 2003).

DECLINE IN NATURAL OR WILD POLLINATORS

Pathogen Spillover

Nosema bombi could be the most important factor responsible for the extinction of *Bombus franklini* (Thorp et al., 2003), perhaps via "patho-

gen spillover” (Colla et al., 2006; Box 3-1), which can occur when heavily infected, domestic hosts interact with closely related wild populations. Commercially produced bumble bees used for greenhouse pollination often have extensive pathogen infections that can spread to wild bees when the commercial bees escape from greenhouses and interact with their wild

BOX 3-1

Unintended Consequences of Greenhouse Pollination and Native Pollinators

When commercial growers began to grow tomatoes in greenhouses, they realized that good fruit set required pollination (Velthuis, 2002). Tomato flowers have poricidal anthers that are typically pollinated by buzz pollination—the vibration of the wing muscles of large bees that land on flowers to collect pollen. Different techniques were investigated to achieve pollination mechanically: blowers were installed to move pollen around, overhead wires used as trellises were struck or shaken, and hand-held electric vibrators were used to shake individual flowers. Introducing bees into greenhouses proved the most economical strategy. Although some pollination can be accomplished by honey bees, bumble bees are much more efficient. In the 1980s, large-scale bumble bee rearing operations began in Europe for use by growers of greenhouse tomatoes and other crops.

Two unintended consequences have resulted from this commercially successful effort. First, because greenhouses are not generally airtight and sometimes are not screened, bumble bees escape and establish in areas of the world where they are not native. The effects have not yet been widely studied, but they are likely to include competition with native bees. Second, the commercial rearing and export of bees has also resulted in transport of bumble bee parasites and diseases, possibly causing the apparent local extinction of *B. occidentalis* from the west coast of the United States in recent years and the disappearance of *B. franklini* from its relatively small range in the area along the Oregon and Washington border.

Because there are no large-scale monitoring operations for bumble bee distribution and abundance, it is difficult to determine the consequences of introducing bees and their diseases. Internal tracheal mites of European origin have been found in wild bumble bees in Japan, and *Nosema bombi*, a microsporidian parasite of bumble bees, has been found in colonies imported from Europe (Colla et al., 2006; Thorp et al., 2003).

counterparts at nearby flowers. In Canada and elsewhere, foraging bumble bees can escape from greenhouses and survive; Whittington and colleagues (2004) reported that as much as 73 percent of the pollen carried by *Bombus* foragers in greenhouses comes from native plants and weeds growing outside, and the European species *B. terrestris* is now established in Japan after its introduction for greenhouse pollination (Matsumura et al., 2004). Managed, greenhouse-reared bumble bees are likely to come in contact with wild *Bombus* species. If extinction of *B. franklini* was caused by pathogen spillover, this species has the unfortunate distinction of providing the first known example of this phenomenon in wild invertebrates; pathogen spillover has been reported in vertebrates and plants (Power and Mitchell, 2004).

Interspecific Competition in Bees

Pollinators have been introduced from one part of the world to another for at least three centuries, resulting in the establishment of one species (*Apis mellifera*) and several species of another genus (*Bombus*) on most continents. Many other introduced species have become established in the United States and Canada (Table 3-1). The major damage caused by introduced species includes competition with native pollinators for floral resources and nest sites (Barthell and Thorp, 1995; Barthell et al., 1998; Thorp et al., 2000; Box 3-2), inadvertent introduction of natural enemies (Butz-Huryn, 1997; Dupont et al., 2004; Kato et al., 1999; Paton et al., 1992, 1996; Roubik, 1978), especially pathogens that can escape into wild populations of native pollinators, enhanced pollination of exotic weeds and furthering their spread by increasing seed set (Barthell et al., 2001; Goulson and Derwent, 2004), and disruption of the pollination of native plants via deposition of heterospecific pollen on the stigma.

The extent to which introduced species disrupt native communities remains equivocal (Goulson, 2003a; Schaffer et al., 1983). Schaffer and colleagues monitored agave blossoms in Arizona before, during, and after the introduction of genetically marked honey bees (Schaffer et al., 1983). They reported that honey bees lowered the available amount of *Agave* pollen and nectar, and their introduction led to shifts in the numbers of foraging native bumble bees and nectar-feeding ants. Short-term effects of interspecific competition have been documented, including beneficial effects to plants (Dick, 2001), but long-term population effects have not been documented.

Honey bees are highly polylectic (they collect pollen from many unrelated plants) and because even a few colonies can collect hundreds of kilograms of nectar and dozens of kilograms of pollen annually (Buchmann, 1996), they can lower the available amount of nectar and pollen in diverse natural plant communities (Paton, 1990, 1993, 1996). The flower-visiting behavior of native flower visitors—such as bees, hummingbirds, ants, and

TABLE 3-1 Exotic Bee Species Now Established in the United States and Canada (Polylectic Species Collect Pollen from Many Unrelated Plants)

Scientific Name	Introduction	Dates
ANDRENIDAE		
<i>Andrena wilkella</i> (Kirby)	Accidental	1700–1800s
APIDAE^a		
<i>Apis mellifera</i> L.	Introduced	1620s
<i>Apis mellifera scutellata</i> Lepeletier	Introduced	1950s
<i>Anthophora plumipes</i> (Pallas)	Introduced	1980s
<i>Ceratina cobaltina</i> Cresson ^b	Accidental	1970s
<i>Ceratina dalltoreana</i> Friese	Accidental	1940s
<i>Centris eisenii</i> Fox ^c	Accidental	1990s
<i>Xylocopa tabaniformis parkinsonae</i> Cockerell ^d	Accidental	1980s
COLLETIDAE		
<i>Hylaeus bisinuatus</i> Forster	Accidental	1990–1910
<i>Hylaeus hyalinatus</i> Smith	Accidental	1990s
<i>Hylaeus punctatus</i> Brulle	Accidental	1980s
MEGACHILIDAE		
<i>Anthidium manicatum</i> L.	Accidental	1960s
<i>Anthidium oblongatum</i> (Illiger)	Accidental	1990s
<i>Chelostoma campanularum</i> (Kirby)	Accidental	1960s
<i>Chelostoma fuliginosum</i> (Panzer)	Accidental	1960s
<i>Hoplitis anthocopoides</i> (Schenck)	Accidental	1960s
<i>Lithurgus chrysurus</i> Fonscolombe	Accidental	1970s
<i>Megachile apicalis</i> (Spinola)	Accidental	1930s
<i>Megachile concinna</i> Smith	Accidental	1940s
<i>Megachile lanata</i> (F.)	Accidental	1700–1800s
<i>Megachile rotundata</i> (F.)	Accidental	1920–1945
<i>Megachile sculpturalis</i> Smith	Accidental	1990s
<i>Osmia coerulescens</i> (L.)	Accidental	1800s
<i>Osmia cornifrons</i> (Radoszkowski)	Introduced	1960s
<i>Osmia cornuta</i> (Latreille)	Introduced	1980s

^a*Ceratina (Pithitis) smaragdula* (F.) was deliberately introduced to California and Florida, but failed to establish (Daly et al., 1971).

^bThe neotropical bee *Ceratina cobaltina* Cresson has been collected sporadically in Texas since 1978 and may be adventive (J. Neff, Central States Melittological Institute, Austin, Texas, personal communication, October 2005).

^cThe centridine *Centris eisenii* has been collected at horticultural plantings of *Callaeum macropterum* (its floral oil host plant) from Nogales to Tucson, Arizona, since the 1990s, and is likely adventive and established in southern Arizona (S. Buchmann, unpublished data).

Distribution	Floral Host	Reference
Northeastern United States, eastern Canada	Polylectic	Malloch, 1918
Global, except polar regions	Polylectic	Smith, 1977
Southern United States, California	Polylectic	Winston, 1992
Maryland	Polylectic	Batra, 1994a, 2003
Texas	Polylectic	Neff, personal communication
California	Polylectic	Daly, 1966
Southern Arizona (Nogales, Tucson)	<i>Callaeum macroptera</i> , <i>Lycium</i> spp.	Buchmann and Snelling, personal communication
Texas (Austin only)	Polylectic	Neff, personal communication
Transcontinental	Polylectic	Snelling, 1970
New York	Polylectic	Ascher, 2001
California	Polylectic	Snelling, 1983
New York, Connecticut, Ontario	Polylectic	Jaycox, 1967
Mid-Atlantic States	Polylectic	Hoebeker and Wheeler, 1999
New York	<i>Campanula</i>	Eickwort, 1980
New York	<i>Campanula</i>	Eickwort, 1980
New York, Virginia	<i>Echium</i>	Eickwort, 1980
New Jersey (now locally extinct?)	<i>Centaurea</i>	Roberts, 1978
Eastern United States, Washington, Oregon, California	Polylectic	Stephen and Torchio, 1961
Transcontinental	Asteraceae	Butler and Wargo, 1963
Florida	Polylectic	Mitchell, 1962
Transcontinental	Fabaceae	Stephen and Torchio, 1961
Eastern United States	Polylectic	Mangum and Brooks, 1997; Batra, 1998
Northeastern and northwestern United States, parts of Canada adjacent to the United States	Fabaceae	Rust, 1974
Transcontinental, patchy	Rosaceae	Batra, 1998
Limited local U.S. releases	Rosaceae	Torchio and Asensio, 1985; Torchio et al., 1987

^dThe larger carpenter bee (*Xylocopa tabaniformis parkinsonae*) is now a permanent resident of the city limits of Austin, Texas, likely having been accidentally introduced (an anthropogenic range extension) in firewood, which may also have been the case with *Ceratina cobaltina*.

SOURCE: Adapted with permission from Cane (2003).

BOX 3-2

Competition Between Managed and Wild Pollinators

If a plant community is close to its carrying capacity for pollinators, introduction of additional pollinators by moving in managed colonies of honey bees or other bees, or the introduction of more native bees, presents the potential for increasing competition for floral resources. This potential for competition has been a concern for areas where honey bees are not native but have been introduced or proposed for introduction, and also for areas (Australia) where bumble bees are not native but have been proposed for introduction. In a literature review in 1997, Butz-Huryn concluded that “the presence of honey bees, however, alters the foraging behavior and abundance of some native fauna on flowers, but no studies have shown detrimental impacts of honey bees on population abundances of any native animals or plants.” More recently, in a combination of observational and experimental studies, Thomson (2006) found that niche overlap between honey and bumble bees reached levels as high as 80 to 90 percent during times of resource scarcity, but only in 1 of 7 months of observation was there a significant negative relationship between them. In an experimental study, however, the mean numbers of bumble bee foragers observed on a given transect increased significantly with greater distance from introduced honey bee colonies. Of the three measures (niche overlap, correlations in abundances, and effects of experimental introductions) that Thomson considered, only the experimental data on forager abundances accurately estimated competitive effects on colony reproductive success.

These studies suggest that it may not be easy to detect competition between pollinators, even if it is affecting reproductive success. If feral honey bee colonies increase again in North America, for example if disease-resistant strains are developed, there may be subtle, unintended, but significant effects on native bees that use the same floral resources. If this alters visitation and pollination rates of native plants, there may be consequences for their populations as well.

wasps—shifted after the experimental introduction of honey bees to a chaparral area in southern Arizona (Schaffer et al., 1979, 1983).

An experimental study in California examined the effects of competition with *Apis mellifera* on colony foraging behavior and reproductive success of a native eusocial bee, *B. occidentalis* (Thomson, 2004). Bumble bee colonies in competition with honey bees experienced increased nectar scarcity and had lowered rates of larval production. Thus, *A. mellifera* can competitively suppress a native bee species that is a known important pollinator. The

competitive effects of introduced pollinators depend on phenology (seasonal timing), abundance, and overlap in resource use. Competition among bees is likely because some bumble bee species have proboscides (“tongues”) that are the same length as the proboscis of *A. mellifera* (Inouye, 1977); proboscis length determines in part the range of plants that can be used as nectar sources (Harder, 1982, 1983, 1986; Stang et al., 2006). After Africanized bees were experimentally introduced into a community of neotropical stingless bees, native bee numbers declined, as did their use of floral resources (Roubik, 1978, 1980; Roubik and Wolda, 2001).

In addition to competitively suppressing native bees, exotic bees can affect ecosystem function by virtue of their foraging habits. Many exotic species demonstrate a preference for visiting the flowers of weedy plants on disturbed sites (Goulson, 2003a; Roubik, 1983; Thorp, 1996) and accordingly can be less likely to pollinate native plant species. Effects of introduced Africanized honey bees on populations of native stingless bees in Central America have been reported by Roubik (1978, 1980). Those studies indicate that the potential of a nonnative pollinator species to affect native populations must be considered before introduction.

Habitat Losses for Insect Pollinators

Habitat alteration, fragmentation, and loss pose major problems for populations of many organisms, and pollinator populations are no exception (Kearns and Inouye, 1997; Kevan, 2001; Kevan et al., 1990). Bees and other insect pollinators require nesting sites (suitable soil, dead wood, abandoned mouse nests, burrows) and floral resources (nectar and pollen) to persist. These environmental resources are at risk through disruption caused by row-crop agriculture, grazing, and fragmentation of habitat into patches too small to support diverse communities of pollinators (Kearns et al., 1998; Kevan, 1999, 2001; Kevan et al., 1990). Changes in agriculture, caused by large plantings of monocultures, loss of field margins, abandonment of crop rotation involving legumes (which have been replaced by fertilizers), and lower diversity of weeds in fields and pastures (caused by herbicide use) are all detrimental to pollinator populations (Goulson, 2003b; Kevan, 1999; Kevan et al., 1990). The loss of flower-rich grasslands, and in particular the long-tubed flowers in the Fabaceae, seems to underlie the decline of at least three previously common bumble bee species in England (Goulson et al., 2005). Grazing can disrupt ground-nesting bees, affect availability of water (for nest construction) and nectar, and decrease the diversity and abundance of floral resources (Gess and Gess, 1993; Vinson et al., 1993). Fragmentation makes it more difficult for pollinators to maintain metapopulation structures, decreasing the availability of corridors and source populations for recolonization. Bumble bees seem particularly susceptible to such effects,

and more than half of the species in the United Kingdom are either already extinct or could face extinction in the next few decades (Goulson, 2003c). The apparent loss of two species in the United States in the past few years suggests that North American bumble bees are similarly imperiled as a result of the combined effects of numerous anthropogenic factors, including habitat loss, degradation, conversion, pesticide use, pollution, and pathogen spillover from commercial bumble bee cultures (Thorp, 2003, 2005).

The urbanization of many pollinator habitats also can have unintended, detrimental consequences. Pollinator populations can be reduced by exposure to city lights and other artificial light sources, including “bug zappers” (Frick and Tallamy, 1996), and by traffic on roadways (McKenna et al., 2001). Some researchers, however, report positive effects of urban or suburban growth on selected bee species when floral resources and nest sites are available (Cane et al., 2006; Frankie et al., 2005).

A decline in habitat quality can occur even if the overall diversity of vegetation is static or increases; floral composition is key to determining suitability. Rasmont and colleagues (2006) suggested that the loss of predominantly longer-tongued bee taxa in Belgium and France is the result of a loss of floral resources, especially plants with long corollas (Fabaceae, Lamiaceae, Scrophulariaceae, Boraginaceae). They also concluded that anthropogenic disturbances—excessive mowing of embankments, road sides, and public areas—could have led to the loss of floral hosts and their specialized bee pollinators. They further hypothesized that decreases in native, solitary, ground-nesting bees could have been caused by afforestation and the negative effects of poisoning or the sublethal effects of exposure to insecticides, fungicides, and herbicides. Afforestation occurred on chalky dry grasslands (prime bee habitats), especially in the Namur province, where habitats have been converted to pine plantations or housing. Bees and other pollinators can survive in urban or suburban settings if nesting sites are available and if there is appropriate floral diversity to provide nectar and pollen throughout the growing season (Cane et al., 2006; Frankie et al., 2005).

Invasive Plant Species and Bees

The literature on biological control is rife with accounts of accidental or even deliberate introduction of plants that have become noxious weeds. In North America, exotic grasses accidentally introduced or grown as livestock fodder are spreading rapidly (D’Antonio and Vitousek, 1992; Larson et al., 2001; Zavaleta et al., 2001). Exotic grasses, such as red brome (*Bromus madritensis*) and buffel grass (*Cenchrus ciliaris*) in the southwestern United States and northern Mexico, are rapidly choking out other plants, decreasing nectar and pollen-producing wildflowers, and providing fuel for intense wildfires. Because buffel grass and other highly invasive grasses cover bare

ground, they provide optimal nesting sites for ground-nesting solitary bees (Buchmann, 1996), but such benefits could be outweighed by elevated risks of wildfires and by reductions in available forage species (Asner et al., 2004; Daehler, 2003).

Bee Genetics and Diploid Males: An Extinction Vortex?

Like the entire order of Hymenoptera, bees exhibit haplodiploidy, in which males develop from unfertilized eggs while females are derived from fertilized eggs. The genetic basis of sex determination in haplodiploid species appears to be diverse (Bull, 1983; Cook, 1993). In some hymenopteran insects, including bees, a complementary sex-determining mechanism is present (Cook, 1993). Females develop when the alleles at the sex determining locus are different (heterozygous). Unfertilized eggs develop into males because they are hemizygous at this locus. And diploid males, which are not viable, arise when the alleles at the sex-determining locus are the same (homozygous). The gene for complementary sex determination (*csd*) has recently been identified in honey bees (Beye et al., 2003), providing strong molecular support for understanding complementary sex determination.

A recent theoretical analysis suggests that complementary sex determination could be a risk factor for the decline, and even extinction, of bee pollinators (Zayed and Packer, 2005). Zayed and Packer (2005) developed a stochastic mathematical model that predicts that if population sizes decrease (because of other intrinsic or extrinsic factors, such as those discussed above), the frequency of diploid males will increase because of inbreeding and the loss of heterozygosity at the *csd* locus. According to this model, the increase in diploid males leads to inbreeding depression, reducing the effective breeding size of a population and decreasing the production of females, thus further depressing populations. Thus, under some conditions, single-locus complementary sex determination can create substantial genetic load.

Support for the “extinction vortex” hypothesis currently is limited. Zayed and Packer (2001) estimated the frequency of diploid drones could be as high as 50 percent in small populations of the primitively eusocial bee *Halictus poeyi* in central and south Florida, much higher than earlier estimates by Kukuk (1989) of 2 to 14 percent. Hedrick et al. (2006) suggested that the deleterious effects of low variation at the *csd* locus in Hymenoptera might be stronger than for self-incompatibility genes or Major Histocompatibility Complex genes; these loci are generally thought to be particularly important in the population dynamics of plants and vertebrates, respectively. The extinction vortex hypothesis is noteworthy because prior to its development, haplodiploid organisms were thought to be relatively less sensitive to genetic factors that can cause population declines, such as the

founder effect (the effect of establishing a new population by a small number of individuals, carrying only a small fraction of the original population's genetic variation), the Allee effect (the positive effect of population density on population growth rate), genetic drift, and deleterious mutations (Hartl and Clark, 1997) because deleterious alleles have a higher probability of being purged in haploid males. But the extinction vortex hypothesis predicts that haplodiploid species with particularly small populations, and thus fewer alleles at *csd*, are particularly at risk (Hedrick et al., 2006). Solitary Hymenoptera have lower fecundity and population sizes than do eusocial species. This novel hypothesis in pollination conservation genetics deserves serious examination (Zayed and Packer, 2005).

Transgenic Crops and Butterflies

Concerns about transgenic crops and nontarget species have been studied most extensively for butterflies, with a particular focus on the influence of “Bt corn.” Initial genetic transformations of corn (*Zea mays*) used *Bacillus thuringiensis* (Bt) endotoxins, specifically Cry1ab, Cry1ac, or Cry9c, for control of the European corn borer, *Ostrinia nubilalis* (Minorsky, 2001). Before the 1996 release of Bt corn, most industry testing focused on nontarget predators and the honey bee, all of which are taxa not expected to be affected by the Lepidoptera-specific toxins (Malone and Pham-Delègue, 2001; O’Callaghan et al., 2005). By 1999, more than 20 million acres (9.6 million hectares) of Bt corn had been planted in the United States—more than 20 percent of all corn acreage (NRC, 2000)—and concerns over consequences to nontarget organisms had increased.

In a small-scale laboratory bioassay, Losey and colleagues (1999) demonstrated that larvae of the monarch butterfly (*Danaus plexippus*) experienced substantial mortality after ingesting Bt corn pollen. Partly because of the iconic nature of the monarch butterfly—its striking appearance and thousand-mile migration to a narrow range of overwintering sites led to its designation as the state insect in Alabama, Idaho, Illinois, Texas, West Virginia, and Minnesota (<http://www.adver-net.com/states.html>)—the discovery of the potential for damage caused by Bt corn led to widespread public alarm (Berenbaum, 2001). The dramatic increase in acreage of transgenic corn between 1996 and 2000 notwithstanding, no documentation of declines in monarch populations, either in the midwestern United States, where much of the nation’s transgenic corn was planted, or in the overwintering sites was reported (see Chapter 2). The implications of the work of Losey and colleagues (1999) were questioned for natural populations (Shelton and Rousch, 1999).

Concern in the scientific community and among the public at large prompted multiple studies to estimate risks associated with monarch butter-

fly exposure to corn pollen and to quantify the effects of pollen ingestion (Hellmich et al., 2001; Oberhauser et al., 2001; Pleasants et al., 2001; Sears et al., 2001; Stanley-Horn et al., 2001; Zangerl et al., 2001). Collectively, the work showed that the asclepiaceous host plants of *D. plexippus* are found in cornfields throughout much of eastern North America, so *D. plexippus* is in fact potentially vulnerable to the consequences of exposure to Bt corn pollen. Despite the proximity of monarchs to transgenic corn pollen, however, the risks of adverse effects are low. A combination of factors provides protection: selection for particular genetic transformations of corn (Hellmich et al., 2001; Zangerl et al., 2001), caterpillar behavior (Anderson et al., 2005), lack of pollen persistence (Pleasants et al., 2001), and phenological displacement (Bartholomew and Yeargan, 2001). Sears and colleagues (2001) conducted a risk assessment on the basis of available laboratory and field data and they concluded that an adoption rate of the demonstrably less harmful Bt corn transformations of 80 percent of the total corn crop would place only 0.05 percent of the monarch population at risk. This estimated risk is substantially lower than the risk presented by pesticides conventionally used for control of European corn borer (Stanley-Horn et al., 2001).

Although the public focus on nontarget effects of genetically modified corn originated with the report on monarchs (Losey et al., 1999), other studies have estimated negligible nontarget effects for a few other Lepidoptera: *Papilio polyxenes*, the black swallowtail (Wraight et al., 2000), and *Euchaetes egle*, the milkweed tussock caterpillar (Jesse and Obrycki, 2002). Laboratory and field studies of Bt corn on other continents (Li et al., 2005) also failed to demonstrate damage to a nontarget lepidopteran, *Antheraea pernyi*, which is used as a natural silk source (Li et al., 2005).

Transgenic crops could pose secondary reasons for concern for pollinators, in the form of genetically modified, herbicide-tolerant (GMHT) crops. Weeds in agricultural monocultures can be important host plants for lepidopteran pollinators (milkweed for monarch butterflies; Oberhauser et al., 2001) and nectar or pollen resources for a variety of pollinator species. They can provide resources for more of the growing season than does the crop, and they attract pollinators that the crop does not (for example, long-tubed corollas for long-tongued pollinators). Evidence for this effect is provided by the British Farmscale Study, a 5-year project that assessed the effects of farm management of GMHT crops on farmland biodiversity relative to conventional agriculture. Heard and colleagues (2003) reported that weed populations were reduced in most (but not all) fields of GMHT crops, and Haughton and co-workers (2003) reported reduced abundances of butterflies in transgenic beet and spring canola fields and smaller numbers of bees in transgenic beet fields compared with non-GMHT crops. In field margins, butterfly numbers were lower by 24 percent adjacent to transgenic

spring canola (Roy et al., 2003). In general, pollinator numbers reflected nectar source abundance (Hawes et al., 2003). Whether the reduced abundances in the field could lead to reduced pollinator populations over time would depend on the proportion of GMHT crops within the foraging ranges of these insects. Moreover, it is not known whether those findings are applicable to agroecosystems outside of Britain.

Habitat Destruction and Bats

Bats face important extinction threats (Chapter 2). Mickleburgh and colleagues (2002) reported that 11 bat species have become extinct in the past 400 years, 65 are either critically endangered or endangered, and 177 more are vulnerable to extinction, according to the criteria of the World Conservation Union (Mickleburgh et al., 2002). The 242 bat species represent about 24 percent of the world's total number of bat species, a proportion that is consistent with the 25 percent of the mammals of the world considered at risk of extinction (IUCN, 1996).

The loss of bat populations is mostly the result of habitat destruction, especially of roosting sites in caves. About half of Mexico's 140 bat species (Arita, 1993; Medellín et al., 1997) and half of the United States' 45 species (Pierson, 1998) roost in caves. Among nectar-feeding bats (12 species in Mexico and the United States), only two do not use caves as roosts (Arita, 1993). The others, including the three migratory species with seasonal ranges in the United States, rely on caves to some extent. Bats spend more than half of their time roosting in caves (Kunz, 1982) and they attain high numbers in cave environments (Tuttle, 2000), so the destruction of caves is a significant threat to bats (Medellín, 2003). Severe declines of cave bat populations have been documented in Mexico and elsewhere (Hutson et al., 2001; Medellín, 2003; Moreno, 1997).

The most common causes for the destruction of cave-dwelling bat populations involve misguided attempts to control the vampire bat (*Desmodus rotundus*), vandalism such as setting fires in caves, disturbance during critical times such as birth peaks, and persecution of such mythical creatures as the chupacabras¹ (Arita and Santos-del-Prado, 1999; Medellín, 2003). These causes are linked to a lack of understanding of the bats' ecological purposes and economic benefits (Medellín et al., 2004).

Habitat destruction also threatens migratory pollinivorous bats. Species that migrate seasonally (Arita and Santos-del-Prado, 1999; Medellín et al., 2004; Wilkinson and Fleming, 1996) need a nectar trail or corridor along their migratory route (Allen-Wardell et al., 1998; Buchmann and Nabhan,

¹Mythical creature said to inhabit part of the Americas (particularly in Puerto Rico) and to attack and drink blood of livestock.

1996; Fleming et al., 1993; Nabhan et al., 2004) that is continuous and sufficiently conserved to provide the bats with resources. Natural habitats have been destroyed or fragmented along the migratory corridors of western Mexico and other areas (Valiente-Banuet, 2002), but it is not known whether the destruction is damaging bat populations.

Some nectar-feeding bats are habitat specialists that could depend largely on the availability of intact dry tropical forest for survival (Quesada et al., 2003). That group includes nectarivorous bats with restricted distributions, such as the Mexican banana bat (*Musonycteris harrisoni*) and the Moreno long-tongued bat (*Glossophaga morenoi*). The bats inhabit the dry tropical forest of western Mexico, a region that has experienced considerable deforestation and fragmentation (Trejo and Dirzo, 2000). Declines in their populations could affect the reproductive biology of their food plants (Quesada et al., 2003).

Habitat Changes and Hummingbirds

Most studies of threats to landbirds have focused on nonhummingbird species (for example, Rappole and McDonald, 1994; Robbins et al., 1989), partly because no hummingbird is included on the U.S. Endangered Species Act list. Migratory bird species (including some pollinating species) show declines that have been linked to deforestation and forest fragmentation in the tropical wintering ranges of those species (Robbins et al., 1989). The Audubon Society's WatchList (<http://www.audubon.org/bird/watch/>) has six species of hummingbird identified by Partners in Flight at the national level as moderately high or moderate priority: the Allen (*Selasphorus sasin*), buff-bellied (*Amazilia yucatanensis*), calliope (*Stellula calliope*), Costa (*Calypte costae*), lucifer (*Calothorax lucifer*), and rufous (*Selasphorus rufus*) hummingbirds. Threats listed for the six species on the WatchList include habitat destruction that results from human encroachment (urbanization, agriculture, conversion of grasslands for cattle ranching). Another important identified threat is the replacement of native plants by invasive species that are unproductive for hummingbirds.

Calder (2004) identified the destruction of stopover habitat—considered critical to migration—along the migratory corridors as a cause of population decline. He also identified habitat destruction attributable to the invasion of African exotic buffel grass, which could damage Sonoran Desert vegetation (Burquez and Martínez-Yrizar, 1997). Abnormal weather, primarily cold winters or drought along desert migratory corridors, also could pose an important threat to hummingbirds (Calder, 2004). After one particularly cold winter (1957–1958), Bailey and Niedrach (1965) reported that less than one-fourth of the 1957 population of broad-tailed hummingbirds reap-

peared in 1958 and 1959. After another unusually cold winter in 1995, the population declined by an estimated 57 percent (Calder, 2004).

At least 7 (5 threatened, 2 endangered) of the 23 hummingbird species are shown on the Mexican list of species at risk of extinction (SEMARNAT, 2002). These seven species were *Campylopterus excellens*, *Lophornis brachylopha*, *Thalurania ridgwayi*, *Hylocharis xanthusii*, *Eupherusa cyanophrys*, *Amazilia viridifrons*, and *Eupherusa poliocerca* (Ornelas, 2000). All face similar threats: they have restricted distributions (all seven are endemic to small areas in the south, west, or northwest of Mexico) and all have experienced severe habitat destruction or fragmentation caused by conversion of grasslands to use for cattle ranching or agriculture. Urban or suburban domestic cats that are allowed outside have been implicated in mortality of ruby-throated hummingbirds, a species of conservation concern in some parts of its range (Lepczyk et al., 2004).

One threat is associated only with the (primarily Mexican) lucifer hummingbird: trade in individuals in past decades (although confirmation is lacking) (<http://audubon2.org/webapp/watchlist/viewSpecies.jsp?id=127>), which is likely to have affected several other species. It is not known whether the hummingbird trade continues to be a factor of concern.

Climate Change

Global, regional, and local climate changes can alter or disrupt plant-pollinator relationships. Included in the global climate change forecast are shifts in temperature and precipitation, concentrations of carbon dioxide (CO₂) and ozone, and ultraviolet light levels. All are important to plant growth and flowering, and those changes could alter plant and pollinator phenology and distribution along altitudinal and latitudinal gradients, generate changes in plant and pollinator mutualisms and community compositions, and cause local extinctions.

There is evidence that the latitudinal and altitudinal ranges of some plants and pollinators have changed in the past 30 years, presumably in response to global warming (Walther, 2004). For example, some butterflies in Britain and North America have expanded ranges north (Crozier, 2003; Hill et al., 1999; Parmesan et al., 1999), and others in Montana (Lesica and McCune, 2004), Spain (Wilson et al., 2005), and Norway (Klanderud and Birks, 2003) have contracted ranges at lower altitudes and latitudes.

An increase in atmospheric CO₂ could alter production of nectar (reviewed by Davis, 2003). Typically, elevated CO₂ concentrations alter nectar volume and secretion rate, sometimes negatively and sometimes positively, but not sugar concentration or composition (for example, Lake and Hughes, 1999). Increases in CO₂ could benefit at least one species of

melon (*Cucumis melo*). Average nectar volumes per flower were significantly higher, sometimes by as much as 100 percent (Dag and Eisikowitch, 2000), in greenhouses enriched with CO₂. No comparable greenhouse or field studies seem to have addressed the potential for CO₂ enrichment to affect pollen production.

Elevated intensities of ultraviolet-B radiation (UV-B; wavelengths between 280 and 320 nanometers) result from diminished concentrations of atmospheric ozone and can delay flowering and diminish lifetime flower production in some plants. Sampson and Cane (1999) reported idiosyncratic responses in flowering phenology and flower production in two annual plants, traits that could affect plant competition for pollinator services, and plant and pollinator reproductive success. Stephanou and colleagues (2000) reported that UV-B increased nectary size in another species, which apparently resulted in an observed increase in pollination, but no differences were reported in honey bee foraging behavior on brassicaceous nectar plants exposed to and protected from UV-B (Collins et al., 1997).

In the Washington, D.C. area, Abu-Asab and colleagues (2001) reported that 89 plant species had advanced flowering time by an average of 4.5 days (although 11 species showed later flowering times). Primack and colleagues (2004) used herbarium specimens of the same individual plants in the Arnold Arboretum in Boston, Massachusetts, to compare flowering times from 1885 to 2002. Plants flowered 8 days earlier from 1980 to 2002 than they did from 1900 to 1920. Flowering by agricultural species also is influenced by global warming: a 40-year study of white clover (*Trifolium repens*) revealed that flowering has advanced by 7.5 days per decade since 1978 (Williams and Abberton, 2004).

Several studies demonstrate that pollinator phenology can be influenced by changing global temperatures. The first appearance of most British butterflies has advanced in the past two decades; peak appearance also occurs earlier, and multibrooded species exhibit longer flight periods (Roy and Sparks, 2000). Forister and Shapiro (2003) documented a similar change in California butterflies. The mean date of first flight trended toward earlier dates for 16 species (70 percent of the fauna studied), and the trend was statistically significant for 4 of them (average shift of 24 days). Seven species showed trends toward later appearance that were not statistically significant. Some Spanish butterflies (8 of 19 species studied from 1988 to 2002) also showed significant advances in mean flight dates (Stefanescu et al., 2003).

If the phenology of flowering and pollinator activities does not change synchronously, there is the potential for disruption of coordinated interactions. Plants might flower before or after the period of seasonal activity of their pollinators and different groups of pollinators might respond differ-

ently to a change in temperature. A record-early spring in Japan resulted in drastic decreases in seed set of two species normally pollinated by bees, but not in two others pollinated by flies (Kudo et al., 2004). A long-term study of life cycles of Mediterranean plants and animals showed that the phenology of plant leafing out, flowering, and fruiting changed at different rates, and all were different from changes recorded for butterfly emergence and the arrival of migratory birds (Peñuelas et al., 2002). The authors suggested that these changes could alter ecosystem structure and function. Migrating pollinators (for example, hummingbirds that overwinter in Mexico and reproduce in the United States) depend on corridors with flowers that bloom at the appropriate times during spring and fall migrations. If the timing of the migration does not coincide with flowering, the plants could suffer a loss of pollinators and the pollinators could face energetically expensive migratory flights with no opportunity to forage and replenish metabolic fuel along the way.

Thus, the evidence indicates that plants and their pollinators could respond differentially to climate change. Depending on the degree of variations in their responses, the consequences of climate change could range from subtle to dramatic. Alterations in nectar abundance or concentration could change the foraging behavior of pollinators, increasing or decreasing pollination of one flower by another of the same plant (geitonogamy); changing the quantities of pollen collected or deposited or the distances that pollen is transported—all can have significant effects on plant mating systems and genetic parameters. Changes in floral abundance could in turn influence the abundance and distribution of pollinators. The loss of synchrony that could result from differential responses in phenology of plants and pollinators could be important and possibly result in the loss of some historical mutualisms or the creation of new ones. It appears that this area of research warrants more attention, in view of the potential for climate change to disrupt plant-pollinator interactions significantly in the future.

The combined effects of climate change and other environmental changes (such as habitat fragmentation) have not been assessed for most pollination systems, but Warren and colleagues (2001) reported that 34 of 46 British butterfly species that might be expected to respond positively to climate warming at their northern climatic range margins in fact declined, as negative consequences of habitat loss outweighed the positive responses to climate warming over the past 30 years. Although half of the habitat generalists that also were mobile species increased their distributions, the other generalists and 89 percent of the habitat specialists declined in distribution, suggesting that the diversity of pollinators could decline substantially in the face of the combined pressures of climate change and habitat loss. The potent combination of environmental changes could cause substantial harm to many plant-pollinator interactions.

CONCLUSIONS

Just as different species of pollinators differ in the degree to which their diversity and populations have declined, the causes that underlie decline vary widely. Some mortality is particularly important in a narrow range of pollinators; in managed pollination systems, there is clear evidence of reductions in pollinator numbers caused by introduced parasites and pathogens. The evidence indicates that these agents of mortality also could operate in wild pollinator declines. Other causes of mortality affect a cross-section of pollinators (albeit to different extents); habitat degradation and habitat loss, in their many manifestations, have contributed to declines in many vertebrate and invertebrate pollinators.

4

Effects of Variations in Pollinator Populations on Pollination Services

Because pollinators provide essential ecosystem services in agricultural and natural areas, it is valuable to determine whether pollination services are threatened by their declining populations. Many plant species rely on pollinators for sexual reproduction, but whether a global “pollination crisis” is jeopardizing food supplies or wild biodiversity has been debated (Buchmann and Nabhan, 1996; Ghazoul, 2005a,b; Potts et al., 2005; Steffan-Dewenter et al., 2005). Chapter 2 noted that a pollinator shortage exists when the demand for pollination services exceeds available pollinator capacity. Shortages can be exacerbated by pollinator declines, but they can arise even when pollinator populations are stable or increasing over time. Some shortages, for example, those caused by the high seasonal demands of the California almond industry for honey bee colonies (for example, Norton, 2005), can be moderated by market forces, like the economics of supply and demand. In contrast, chronic and continuing pollinator declines could threaten the basic ecosystem services that many people take for granted. In the study of consequences for pollination and ecosystem services, it is useful to distinguish between transient pollinator shortages and declines.

POLLINATORS IN AGRICULTURE

Food Security and Nutrition

An evaluation of experimental evidence for pollination requirements of 107 globally traded fruit and vegetable crops (representing 40 percent of global plant-based food production) by Klein et al. (2007) shows that

animal pollination improves production in 75 percent of the crops studied. Most cultivars of another 10 percent of the crops require animal pollination. Another 8.5 percent of the crops do not benefit from animal pollination and its role in production of the remaining 6.5 percent crops is not known. Many crops, however—notably the staple grains that form the foundation of most human diets (rice, wheat, maize, sorghums, millets, rye, barley)—are self-pollinating or pollinated by the wind. Together, species that do not rely on pollinators account for most of the world's food supply by weight (FAO, 2005).

Pollinator declines, therefore, do not fundamentally threaten the world's caloric supplies. However, fruits and vegetables, which add diversity to the human diet and provide essential nutrients, tend to depend heavily on pollinators (Prescott-Allen and Prescott-Allen, 1990; Roubik, 1995). Seven of the nine crops that provide at least 50 percent of the vitamin C available to the human diet globally depend partially or entirely on animal pollination for the production of fruits or seeds (oranges, cabbages, green peppers, tomatoes, melons, tangerines, watermelon) (FAO, 2005; Free, 1993; McGregor, 1976; USDA-NASS, 2006b).

Animal-pollinated crops also tend to have greater economic value than do crops that are not animal-pollinated, and they provide relatively more income to farmers per unit of land (USDA-NASS, 2006b). Moreover, several oilseed crops depend on pollinators, and bee pollination is required to produce the seeds of major forage and hay crops, such as alfalfa and clover, that feed the animals that supply meat and dairy products. Thus, despite the fact that they do not provide the bulk of the human diet, animal-pollinated plants contribute importantly to the quality of the human diet. Although estimates of the proportion of the human diet that is attributable to animal pollination are occasionally attempted and frequently cited (for example, McGregor's 1976 estimate that one-third of the human diet can be traced directly or indirectly to animal pollination), the proportion likely varies among countries and regions and depends on dietary preferences, seasonal availability, cultural practices, and economic status of consumers.

Major Crops

Plant species grown as agricultural commodities display a wide variety of breeding systems. Some readily self-pollinate; others are dioecious, monoecious, or self-incompatible and require animal pollination (Free, 1993; McGregor, 1976; Table 4-1). Dependence on pollinators also varies greatly among crops. In the United States, about 130 agricultural crops benefit from insect pollination (McGregor 1976; see examples in Table 4-1). Most North American crops can produce some fruits and seeds without animal pollination, but pollination often increases their value through higher yields or im-

TABLE 4-1 Value of Common Crops That Require or Benefit from Insect Pollination

Commodity	Bearing Acres	Production Unit	Utilized Production (thousand units)	Value of Utilized Production (\$ thousand U.S.)
Apple	395,000	Ton	4,261.6	1,783,952
Blueberry, cultivated	41,720	Ton	94.4	221,610
Blueberry, wild	NA	Ton	40.2	28,540
Cranberry	39,600	Ton	309.2	208,025
Cherry, sweet	73,940	Ton	246.8	344,471
Cucumber, fresh	58,600	Hundredweight	55,000.0	187,391
Melon, cantaloupe	86,000	Hundredweight	22,107.0	371,721
Melon, watermelon	149,600	Hundredweight	38,208.0	342,918
Nut, almond	550,000	Ton	833.3	1,600,144
Peach	145,530	Ton	1,205.1	454,532
Pear	64,150	Ton	922.5	270,385
Squash, all	50,700	Hundredweight	7,685.0	197,020

SOURCE: Data from NASS Non-citrus Fruits and Nuts 2003 Summary.

proved quality (Klein et al., 2007). Coffee self-pollinates, but yields increase as a result of pollinator visits (Klein et al., 2003a,b,c; Ricketts et al., 2004; Roubik, 2002). A few U.S. crops—melons, cucurbit squashes, almond, and most pome fruits—are completely dependent on animal pollination to set fruit. Crops with many-seeded fruits, such as watermelon, pumpkin, and kiwi, have hundreds of ovules so they require many pollen grains per stigma. Thus, they are more susceptible to pollinator shortages than are those with few seeds per fruit (Free, 1993; Stanghellini et al., 1997).

In a detailed 1976 report, *Insect Pollination of Cultivated Crop Plants*, published by the U.S. Department of Agriculture, McGregor (p. iv) noted that “the pollination of plants, essential in the perpetuation of most species, is so unobtrusively accomplished that it is often overlooked.” Although pollinators are critical to many agroecosystems, their importance varies not only among crop species but even among varieties of the same crop. In addition, wild-pollinator abundances can fluctuate dramatically among locations and over time (Kremen et al., 2002b; Price et al., 2005). Reliable data on the specific contributions of pollinators to crop yields are often lacking, and obtaining this information requires large-scale, long-term studies. Listed in Table 4-1 are the relative area and value of several major crops known to benefit from pollinators. Because managed honey bees are often used to pollinate them, the extent to which managed and unmanaged pollinators provide adequate pollination service for optimal yields remains for the most part undetermined.

Managed and Wild Crop Pollinators

Crop plants in North America are pollinated by many wild or managed native species of animals, in addition to managed colonies of introduced honey bees (*Apis mellifera*). The wild species include native bees, feral honey bees, other insects, birds, and bats (Free, 1993; Chapter 2). For some crops, one or more wild species could be more efficient than honey bees, although honey bees also might contribute to pollination (Free, 1993). Blueberry, cranberry, and kiwi are “buzz-pollinated”—a visiting bee vibrates its body to sonicate the pollen grains out of the flowers’ anthers. Bumble bees (*Bombus* spp.) and some other native bees are much more efficient blueberry pollinators than are honey bees because they buzz-pollinate (Buchman, 1983; Cane and Payne, 1990; Javorek et al., 2002; MacKenzie, 1997; MacKenzie et al., 1996), whereas honey bees cannot. However, honey bees are used to pollinate wild blueberries because apiculture is well developed. Even in crops that are routinely pollinated by managed honey bees, wild pollinators also can contribute pollination services. Watermelon growers in California use managed honey bees, but their crops also receive substantial pollination from a diverse community of native bees (Kremen et al., 2002a).

The adequacy of pollination services provided by managed and wild pollinators, including feral honey bees, can vary widely and is poorly documented for many crops (Free, 1993). Greenleaf and Kremen (2006b) studied field-grown tomatoes for which growers did not import honey bee colonies. They found that native bees (such as *Anthophora* spp. and *Bombus* spp.) were buzz-pollinating the crops. Although wild species are either known or likely to be important pollinators in many crop systems, the relative contributions of different groups of pollinators to crop yields are rarely defined. With such a paucity of relevant research, it is useful to review evidence from a sample of well-studied crops to evaluate the availability and importance of wild pollinators. For these exemplars, pollinator shortages often can be overcome by providing sufficient numbers of managed pollinators, especially honey bees, although in a few cases the crop production depends completely on specific pollinators (for example, midges or bats).

Watermelon

Watermelon (*Citrullus lanatus*) is grown in several parts of the United States and Mexico. U.S. production in 2005 was worth \$410 million (USDA-NASS, 2006b). Because watermelon has separate male and female flowers, animal pollination is critical. Watermelon pollination requirements are high: 500–1,000 pollen grains must be deposited on stigmas to produce marketable fruits (Adlerz, 1966; McGregor, 1976), so the plant relies on multiple insect visits to each female flower for successful pollination (Stanghellini et al., 1997). In most areas of cultivation within North America, pollination

is provided by managed honey bees and a diverse set of native bee species (Kremen et al., 2002a).

In the central valley of California, Kremen and colleagues (2002a) measured pollination at 14 watermelon farms that differed in degree of isolation from natural habitat. At farms near natural habitat, the native bee community was sufficient to provide adequate pollination. At farms far from natural habitat, however, average pollen deposition by native bees alone was insufficient. The inadequacy was the result of a reduction in overall pollinator abundance and of local extinction of the most efficient pollinators (Kremen et al., 2004; Larsen et al., 2005).

Blueberry

Blueberries (*Vaccinium* spp.) grow in several Canadian provinces and in several U.S. states. High-bush blueberries are actively cultivated; low-bush blueberries are harvested from semicultivated wild plants. In the United States, about 44,000 acres (17,800 hectares) of high-bush blueberries are planted to produce a crop worth more than \$275 million annually (USDA-NASS, 2006b). Like many other species in their family, blueberries are buzz-pollinated, primarily by bumble bees (Buchmann, 1983; Free, 1993). Introduced honey bees do not buzz-pollinate, so high-bush blueberries depend largely on native wild bees for pollination (Buchmann, 1983; Free, 1993; MacKenzie, 1997; MacKenzie et al., 1996).

Several research groups have investigated the dependence of blueberry production on wild bees. Cane and Payne (1988), for example, listed four species of wild bumble bee (*Bombus* spp.) and the anthophorine *Habropoda laboriosa* that buzz-pollinate high-bush blueberry fields in Alabama and Georgia. Honey bees from colonies at field borders were found to carry little or no blueberry pollen. In New Brunswick, Canada, pesticide applications in nearby forests were followed by devastating reductions in native populations of bumble bees, andrenid bees, and halictid bees, which might have contributed to a severe drop in low-bush blueberry production (Kevan, 1975b). When a less harmful insecticide was introduced, native bees appeared to recover (Kevan et al., 1997), and production returned to normal (Kevan and Plowright, 1995). These findings highlight both the dependence of the crop on wild pollinators and the interconnectedness of contiguous natural and cultivated habitats.

Sunflower

Sunflowers are grown throughout the world for oil and confection seed, and in 2005, 2.7 million acres were under production in North America, mostly in the United States (FAO, 2005). Sunflower, *Helianthus annuus*,

is a widely distributed native plant in North America, visited by many of its native pollinator species, including some bee species that specialize on sunflower pollen (for example, *Svastra obliqua*). Unlike the sunflower, many crops are grown outside their native ranges and therefore are visited by novel pollinators. The sunflower head consists of many individual florets, each of which passes first through a male stage and then a female stage (Free, 1993). Although the plant is self-compatible, bees often increase sunflower seed set by moving pollen from male-stage florets to female-stage florets within the same flower head and through cross-pollination between individual plants (Greenleaf, 2005; Greenleaf and Kremen, 2006b). Most sunflower varieties are sold as hybrid seeds, which require cross-pollination between pollen-producing lines and those that lack pollen. The hybrid sunflower seed production industry is worth \$26 million annually in the United States (Greenleaf, 2005), and more than 90 percent of seed production occurs in northern California (Lilleboe, 2000).

Several studies have documented improvements in sunflower seed production as a result of insect pollination, although the degree of improvement varies among cultivars. For example, seed set on flower heads increased from 1 to 35 percent when bees provided self-pollination, transferring pollen among florets; when bees moved pollen between florets on different sunflower heads, seed set increased to 63 percent (Free, 1993). Although managed honey bee hives are stocked in hybrid sunflower fields in the United States, non-*Apis* bees also pollinate hybrid sunflowers and might do so far more efficiently than honey bees (DeGrandi-Hoffman and Watkins, 2000; Greenleaf, 2005; Parker, 1981). Non-*Apis* bee interactions with honey bees increase the pollination efficiency on hybrid sunflower by as much as five times, by disturbing them as they forage on florets and causing them to move among plants more often and cross-pollinate plants more effectively (Greenleaf, 2005). From those findings, Greenleaf (2005) calculated that the direct pollination provided by wild bees nationally to the hybrid sunflower seed industry was worth \$1.9 million, the interspecific interaction between wild and honey bees was worth \$10.4 million, and the direct contribution of honey bees was worth \$13.8 million. Both proximity to natural habitat and crop rotation practices affect the amount of sunflower pollination provided by wild bees (Greenleaf, 2005; Greenleaf and Kremen, 2006b).

Canola

Canola is Canada's fourth largest crop in terms of area under cultivation, and annual exports are currently worth more than \$2 billion Canadian (Morandin and Winston, 2005). The two species in the mustard family grown to produce canola oil, *Brassica napus* and *B. rapa*, differ in dependence on pollinators. *B. napus* is self-compatible, but some cultivars

produce better yield with cross-pollination (Kevan and Eisikowitch, 1990). In contrast, *B. rapa* is self-incompatible and therefore requires pollinators for seed set. Although managed honey bees are used, many native species also pollinate canola crops (Morandin and Winston, 2005).

Morandin and Winston (2005) studied pollination of self-incompatible canola in Alberta, Canada, and compared results from fields with different management regimes. They reported that farms with more wild bees also showed smaller pollination deficits, which were defined as the extent to which yields were depressed because of insufficient pollination. The farms with the fewest bees were those planted in genetically modified, herbicide-resistant plants. Because those fields were treated heavily with herbicides, they had a lower diversity and abundance of flowering weeds, which could account for their reduced capacity to support wild bees. Using those results, Morandin and Winston (2006) calculated that profits lost by retiring up to 30 percent of the field area from production would be more than offset by increased yield that would result from better pollination by the more diverse and abundant pollinators found in fields within 750 meters of uncultivated areas.

Coffee

Coffee (*Coffea arabica* and *C. robusta*) is grown extensively in Mexico and is one of the developing world's most valuable export commodities. Worldwide, 11 million hectares are planted in coffee, and the industry employs 25 million people (O'Brien and Kinnaird, 2003). *C. arabica*, the species thought to produce the highest-quality coffee, self-pollinates, but yields increase 15 to 50 percent when flowers are visited by bees (for example, Free, 1993; Klein et al., 2003b; Roubik, 2002). Despite that, few coffee farmers recognize pollination as an issue for their crops (Ricketts et al., unpublished data).

Several recent studies have investigated the importance of wild bees to coffee production. Ricketts and colleagues (Ricketts, 2004; Ricketts et al., 2004) reported that in Costa Rica a diverse community of wild bees pollinates coffee. The pollinators were mainly wild Africanized honey bees and 10 species of social stingless bee (tribe Meliponini). The species depend on forest habitat for nest sites and food resources but flew into nearby coffee fields when they were in flower. Coffee fields near forest patches received more visits by a more diverse set of bees and had 20 percent higher yields than did fields more than 1 km away from a forest. Klein and colleagues (Klein et al., 2002, 2003c) also noted a diverse community of wild coffee pollinators in Indonesia. They reported that coffee yields increased with increased diversity of pollinators and that pollinator diversity increased near forest remnants and in less intensive farms managed with a more diverse

canopy of shade trees. Although these studies were performed outside North America, their findings are informative for coffee production in Mexico.

Cacao

Chocolate is made from the seeds of the cacao tree (*Theobroma cacao*), which is native to the western Amazon basin, but now grown in many humid tropical regions, including Mexico (Clay, 2004). Cacao trees can be either self-compatible or self-incompatible, but even self-compatible trees require insect visits to move pollen from anthers to stigmas and pollinate the flowers. Honey bees do not appear to be effective pollinators (Free, 1993). Although the identity of the principal pollinators of cacao eluded growers and scientists for many years, midges in the family Ceratopogonidae have been identified as the most important group (Free, 1993; Young, 1985). Many other wild insects also have been observed visiting cacao (bees in the subfamilies Halictinae, Meliponinae), but their pollinating efficiency is either low or undetermined (for example, Young, 1981, 1985).

There is substantial evidence that farm management practices influence the amount and quality of habitat for midges within and around cacao farms and therefore can affect yields (Free, 1993). Midges prefer shady, moist conditions; their eggs are laid and larvae develop in rotting wood and leaves on the ground (Free, 1993). Young (1982, 1986) showed that adding pieces of rotting wood to the leaf litter within cacao plantations increased the abundance of several midge species and that cacao plants near shade trees or rotting material often had more fruits than did trees that were farther away.

Agave

Tequila—one of several alcoholic beverages derived from agave—is produced exclusively from *Agave tequilana* var. *azul* in select regions of Mexico. Tequila revenues were close to \$1 billion in exports and domestic sales in 2000 (Tequila Aficionado, 2001), and in 1998, Mexico had about 100,000 hectares (about 250,000 acres) containing roughly 200 million plants (Ramírez, 1998). After 1989, and at least until 2002, the tequila industry faced major agave shortages caused by several diseases that affected about 30 percent of the plants at different stages of development (Jiménez-Hidalgo et al., 2004; Larrea-Reynoso, 1998; Valenzuela-Zapata, 1994).

Although many species of agave, including *A. tequilana*, are naturally pollinated by bats and other animals (Arizaga et al., 2002; Rocha et al., 2005), the industry uses only asexually reproduced plants to replenish the producing population. This practice has prevented outcrossing of individuals and resulted in loss of genetic diversity compared to other agaves (Dalton,

2005). Recent studies have suggested links between the disease outbreaks to this reduction of genetic diversity (Valenzuela-Zapata and Nabhan, 2004), and producers are supporting research to find solutions (Dalton, 2005). The tequila industry very likely would benefit if genetic diversity were maintained and used in various combinations in the fields. Monocultures with little genetic variation are susceptible to pests and diseases.

Other Crops

Ecologists have investigated a variety of crops, both in North America and elsewhere, to determine the degree of pollination services provided by wild bees. Some studies demonstrate extensive pollination by wild pollinators (Roubik, 1993, 1995), whereas others find little support for this assertion (reviewed in Free, 1993; Klein et al., 2007). Additional studies on pollination of muskmelon (cantaloupe), almond, and tomato in California, New Jersey, and elsewhere are under way (Greenleaf and Kremen, 2006a; Kremen, unpublished data; Williams and Kremen, unpublished data; Winfree et al., 2006). The growing body of research will contribute to elucidating the degree to which wild pollinators benefit agricultural production and, more important, the circumstances and management regimes that affect pollination of crops by unmanaged wild pollinators.

Alleviating Pollinator Shortages

Traditional farmers and plant breeders have developed new cultivars that depend less on pollinators. Cultivated hybrid sunflowers (*Helianthus annuus*) self-pollinate even though their insect-pollinated wild ancestors are self-incompatible (Heiser, 1954). In the early 1900s, strawberries were developed with hermaphrodite flowers to improve fruit set (McGregor, 1976), although they still benefit from pollinators. Similarly, flowers of wild tomatoes and some heirloom tomato varieties must be visited by bumble bees to set fruit. Most cultivated tomatoes can self-pollinate if they are jostled mechanically (McGregor, 1976), but greenhouse tomatoes typically are buzz-pollinated by managed bumble bees (Box 3-1). In field production, some varieties of tomatoes also produce more and larger fruits if they are visited by bees (Greenleaf and Kremen, 2006a).

Bananas and some varieties of pineapple, grape, citrus, cucumber, and persimmon can produce fruit without sexual fertilization, a process known as parthenocarpy. Parthenocarpic fruit production solves problems associated with insufficient numbers of pollinators by bypassing them altogether. Parthenocarpy can be induced with the use of plant hormones and genetic modification (Gorguet et al., 2005; Pagnotta, 1999; Rotino et al., 1997). Mainland and Eck (1968) induced fruit production in blueberries with

applications of auxin, gibberellin, and kinin, and Hayata and colleagues (1995) and Maroto and colleagues (2005) used plant regulators to induce parthenocarpic fruit production in watermelons. In a report that detailed parthenocarpy induced by genetic modification, Acciarri and colleagues (2002) reported improved fruit production in eggplant using the *DefH9-iaaM* auxin-synthesizing gene. Donzella and colleagues (2000) reported the same results. Mezzetti and colleagues (2002a,b, 2004) used the *DefH9-iaaM* gene to induce parthenocarpic fruit production in strawberry and raspberry cultivars. Barg and colleagues (2001) reported successful production of parthenocarpy in tomato cultivars by use of a chimeric transgene. Conventional and molecular techniques have been used to produce parthenocarpic cultivars of citrus (Koltunow et al., 2000). The development of additional parthenocarpic varieties through traditional breeding or recombinant DNA techniques could expand the number of crops that do not require pollination by animal vectors. Nonetheless, pollinators contribute to maintenance of plant genetic diversity (see Agave example above) and are important for breeding programs (such as hybrid or other seed production).

In some cases, the problem of insufficient cross-pollination can be addressed by better planting designs. For example, apples are self-incompatible and require cross-pollination not only between individuals but also between cultivars, and movements of honey bees from tree to tree are limited. Using genetic markers, Kron and colleagues (2001a,b) demonstrated that intercultural pollen movement by pollinating honey bees in orchards of dwarf apple was limited to about four neighboring trees. Thus, plantings with too many rows of the same cultivar produced lower yields. In such a situation, the efforts of the pollinators (and the money spent by grower) are wasted, and in essence a pollinator shortage is created unnecessarily. Moreover, Kron and colleagues (2001a,b) noted that the pollen of some apple cultivars is more vigorous than is that of others. Planting arrangements can be designed to increase the efficiency of available pollinators. Another method of alleviating pollinator shortages is to protect and enhance the habitats of wild pollinators. Strategies for improving pollinator habitats in and around agricultural areas are discussed in Chapter 6.

Economic and Financial Consequences of Pollinator Shifts

Honey bees are responsible for the greatest percentage of agricultural pollinator activity in North America, and they constitute the greatest percentage of the commercial pollination market. Commercial beekeepers, who account for an estimated 99 percent of all reported pollination rentals in North America (Burgett, 2004), earn their income from pollination fees and honey sales. Honey revenues averaged \$143 million annually from 1986 to 2005 (USDA-NASS, 1995, 1999, 2004b, 2005), and reached record highs

in 2002–2003 (USDA-NASS, 2005). Although pollination fee data are not reported nationally, the total has been estimated at \$150 million: \$75 per hive for each of the 2 million hives in commercial hands (Rucker et al., 2005).

Commercial beekeepers divide their honey bees' time between crops that contribute to pollination income and crops that yield marketable honey. Honey production is high for alfalfa, clover, and vetch crops. Almonds, however, which create North America's greatest demands for managed honey bees, do not provide commercially competitive honey. Pollination fees tend to be higher for crops that need pollination, but produce poor honey. Burgett and colleagues (2004) reported average pollination fees for honey crops (vetch seed, crimson clover seed, red clover seed, radish seed, blueberry) between 1987 and 2002 ranged from \$2.67 to \$23.29 per colony, in 2002 dollars. By contrast, fees for nonhoney crops (cucumber, pear, sweet cherry, squash, apple, cranberry, almond) were higher: \$25.21 to \$38.24. Rucker and colleagues (2005) reported that honey production and pollination services tend to compete for beekeepers' services and higher honey prices are associated with higher fees for pollination.

The largest concentrations of honey bee colonies are maintained in four regions: the Dakotas and the northwestern tier states, where large areas of vetch and clover produce high-quality honey; California, with almond, fruit, and melon crops; Florida, with orange blossom as the major March and April crop and with winter vegetables and small fruits; and Texas, with winter vegetables (USDA-NASS, 2006). The mobility of commercial bee colonies on tractor trailers creates three major south-to-north pollination routes: West Coast, Midwest, and East Coast.

The economic consequences of pollinator shortages in agriculture hinge on six determining factors: a specific need for animal pollination, a crop yield gain contributed by the pollinator, the crop price, the cost of pollination services, the value of marketed byproducts (such as honey), and the availability of alternative means of pollination.

Predicting the direct, short-run economic consequences of population declines in honey bees—the principal managed pollinator species—is not straightforward. Microeconomic theory predicts two effects; both increase pollination fees. The first is a rise in cost of producing and maintaining commercial bees. This increase reduces the quantity of pollinators that can be supplied at any price (leftward shift in the supply curve, illustrated in Figure 4-1). The second is an increase in demand for commercial honey bee pollination caused by decreases in feral bee colonies and native pollinator numbers or by an increase in acreage or floral density of pollinator-dependent crops (rightward shift in the demand curve, Figure 4-1).

The economic effects of a decrease in abundance of insect pollinator are likely to be greatest for crops that rely heavily on insect pollination. Morse

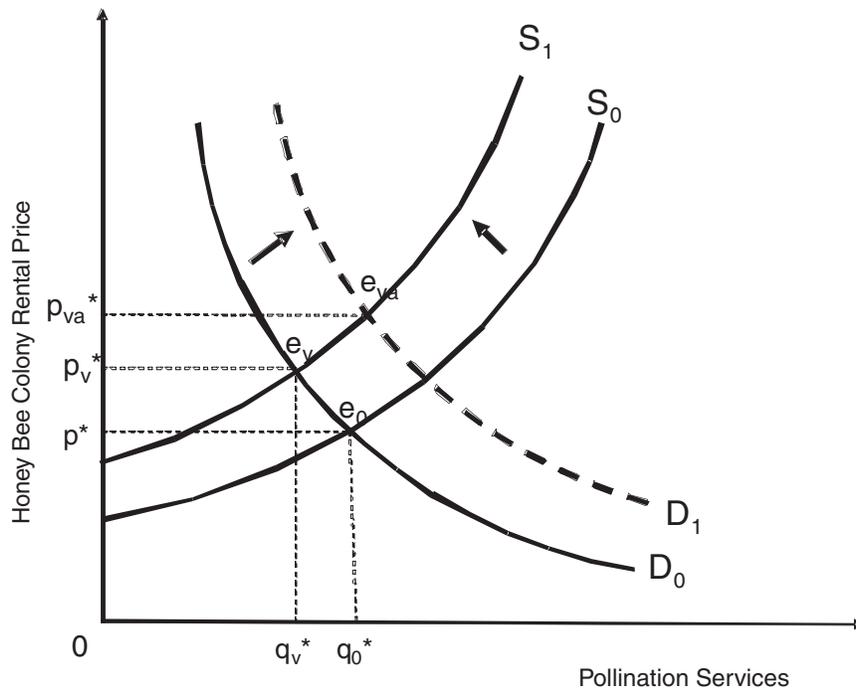


FIGURE 4-1 Honey bee population declines raise bee production and maintenance costs, reducing the commercial supply of pollination services offered at all price levels from S_0 to S_1 , and raising the market price and reducing the marketed quantity of honey bee colony rentals from e_0 to e_v . Agricultural demand for pollination services could rise (from D_0 to D_1) as feral honey bees and native pollinators decrease in abundance or as crop acreage rises (as in almonds), increasing both the equilibrium price and the quantity to point e_{va} .

and Calderone (2000) estimated that five major fruit crops are 100 percent reliant on insect pollination: almond, apple, avocado, blueberry, and cranberry (see Box 4-1). Most calculations of the value of pollination services use current market prices (for example, Morse and Calderone, 2000). However, if a major decrease in pollinator availability were to occur, the prices of crops that depend on pollination would rise, increasing the economic value of the remaining pollination services (Southwick and Southwick, 1992) and reducing consumer welfare (Kevan and Phillips, 2001). The combination of rising production costs and falling yields also could prompt financially marginal producers of pollination-dependent crops to exit the industry or shift to crops that do not depend on pollinators. Both increased food costs

BOX 4-1

Pollination Fees for California Almonds

The California almond industry is contending with record high prices for rentals of honey bee colonies. Average fees jumped from \$35 per colony in the late 1990s to \$75 in 2005 (Burgett, 2005; Burgett et al., 2004) (Figure 4-2), and fees can go as high as \$150 per colony (<http://beesource.com/pov/traynor/bcnov2005.htm>). Given that the U.S. commercial honey bee population remained fairly stable (on a year-to-year basis) between 1996 and 2004 (USDA-NASS, 1999, 2004a, 2005), the increased cost cannot be attributed solely to honey bee decline.

Three other factors are also responsible for the higher pollination fees. First, California almond acreage expanded more than 35 percent (from 405,000 to 550,000 acres) between 1991 and 2004, during which time varroa mites infestations were widely detected (Pollack and Perez, 2005). The current bearing acreage in almonds requires 1.4 million colonies for pollination during the February flowering period (Heinz, 2005), and that figure constitutes more than 60 percent of the U.S. supply of commercial honey bees. Second, honey bee colonies have experienced significant winter mortality that is attributable to varroa mite infestation that leads to seasonal colony shortages each February because beekeepers have not had time to rejuvenate colonies. Third, the price of honey has been relatively high since 2002. Almond nectar is bitter, so beekeepers who market honey avoid almonds as forage plants. Indeed, honey traditionally competes with pollination for the beekeeper's business: when honey prices go up, pollination rental fees climb as well (Rucker et al., 2005).

How high can almond pollination fees go? Recent almond plantings mean that bearing acreage will continue to rise. Given that almonds are almost

and reduced agricultural employment would have negative multiplier effects in the reduction of spending on other goods and services.

The prices of pollination byproducts and the availability of alternative means of pollination also should be considered. A decline in managed honey bee populations should trigger a rise in the price of honey. And the rising cost of pollination and the income lost as a result of lower crop yields should trigger research and development of alternative means of pollination.

Evidence suggests that some of the hypothesized economic effects of pollinator decline have, in fact, occurred in the United States since the mid-1980s when tracheal and varroa mites began to spread. Statistical regression analysis of annual pollination fee data from Washington and Oregon shows that honey bee colony rental fees for pear, cherry, and apple rose by \$4.40–\$5.30 (in 2002 dollars) after 1991, when the varroa mite was widely

entirely dependent on honey bee pollination, with average yields of 1 ton per acre in 2004 and prices ranging from \$1 to \$2 per pound (Pollack and Perez, 2005), even if commercial honey bees contributed only half of the yield, it would be worthwhile for growers to pay \$250–\$500 for each of the 2 to 2.5 hives per acre typically recommended—well above today’s highest usage.

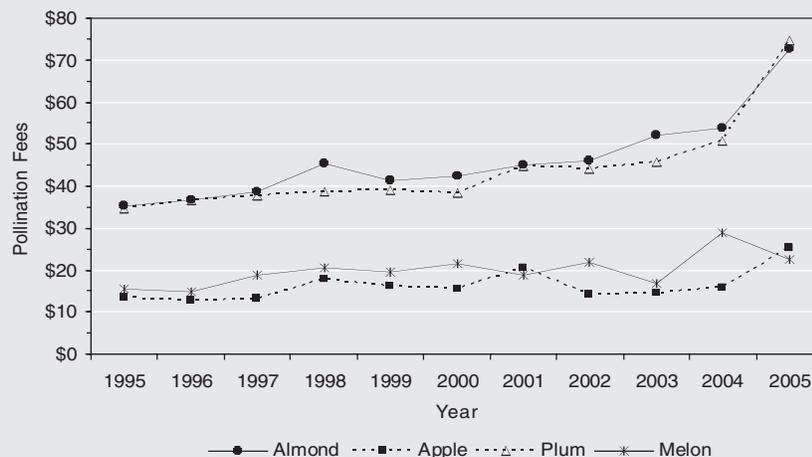


FIGURE 4-2 Honey bee colony rental rates for selected California crops, 1995–2005. SOURCE: Data compiled from *California Bee Times*, various issues, 1996–2006.

detected in the Pacific Northwest (Rucker et al., 2005). As noted by Burgett and colleagues (2004), if each honey bee colony is rented out two to three times per year, the increase in pollination fees roughly equals the estimated annual cost of varroa mite control at \$10–\$15 per colony. By extrapolation from their Pacific Northwest data to the 2 million commercial hives in the United States, varroa mite control has increased honey bee colony rental fees by nearly \$30 million annually (ignoring any honey or crop yield losses that could result from honey bee shortages).

The rising cost of varroa mite control and the high prices of domestic honey during 2002–2003 (Figure 4-3) might also be responsible for the subsequent increase in honey bee pollination fees in 2003–2005. The rise in pollination fees was aggravated by the hard winter of 2004–2005, which caused a 5.7 percent decline in the reported U.S. honey bee population

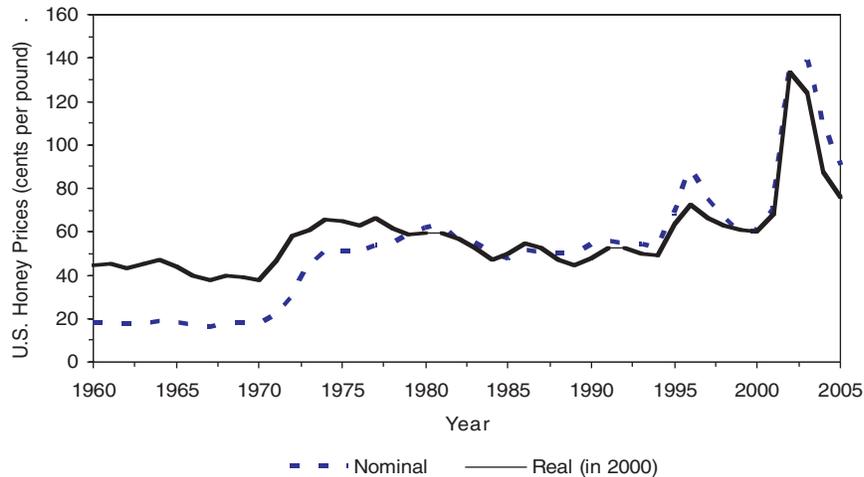


FIGURE 4-3 U.S. honey prices (cents per pound) in nominal and real (2000) terms. SOURCES: Data compiled from prices listed by Hoff and Phillips (1989); USDA-NASS (1995, 1999, 2004b, 2005, 2006); producer price index data for farm products from the Council of Economic Advisors (2006).

(USDA-NASS, 2006). In response to the early season shortage of honey bee colonies, beekeepers imported “package” honey bees from Australia for the 2005 California almond pollination as substitutes for domestic honey bees (Sumner and Boriss, 2006; USDA-APHIS, 2004).

The U.S. commercial honey bee population was stable from 1996 to 2004, but if it were to continue to decline at the rates exhibited from 1947 to 1972 and from 1989 to 1996, it would vanish by 2035. Although that is conceivable, there are strong incentives to protect honey bees and, failing that, to develop alternative methods of pollination. The long-term economic consequences of resumed honey bee population decline will depend on how farmers, beekeepers, scientists, and others respond to smaller populations and higher fees. Writing about almond pollination, pomology consultant Wesley Asai predicted that “growers will have greater interest in new varieties that are self-fertile and possibly even self-pollenizing to reduce dependence on bees” (2005). Agricultural research has a long history of innovation (Hayami and Ruttan, 1985), and new work could focus on mite control, bee tolerance of mites, or crop pollination needs. Another potential response is the introduction of substitute pollinators—propagated bumble bees or the imported Australian packaged honey bees, like those used to pollinate California almonds in 2005 (Sumner and Boriss, 2006). Of course, a new long-term market equilibrium could be established with

higher pollination fees that eventually would be seen in higher prices at the supermarket.

Over the long term, the indirect effects of honey bee shortages will depend on how markets and technology respond. If the pollination markets adjust to a new, higher price equilibrium, then higher costs could undermine the profitability of crop production in marginal areas. Increased food prices also are possible, although whether they occur would depend on competition from fruit, nut, and vegetable producers outside North America.

POLLINATORS IN NATURAL AREAS

Pollinator Limitation of Seed Production

As with agricultural systems, pollinator limitation in natural plant populations occurs through a variety of mechanisms that decrease pollinator abundance below that required by plants for full reproduction, and pollinator shortages are expected to depress fruit and seed set in local plants. Low seed set can be caused by other factors as well, including severe weather, inadequate concentrations of soil nutrients, disease, damage caused by herbivores, partial sterility, or shortages of neighboring plants with compatible pollen. Thus, in plant populations where reproduction is low or appears to be declining, explanations other than inadequate pollination should first be ruled out (Figure 4-4). It is difficult to study the efficacy of pollination services because it is usually impossible to augment native pollinator populations artificially in controlled experiments (Thompson, 2001). Therefore, many studies rely on indirect evidence, such as correlations between pollinator abundance and seed set or the effects of hand-pollination treatments on seed set (Box 4-2).

In the most extreme examples of pollinator limitation, seed set fails because a plant's primary pollinators are extinct or in precipitous decline. The best known cases in the United States involve endemic Hawaiian plant species that depend on pollinating birds or moths that are now extinct on one or more islands (Nabhan and Buchmann, 1996); some of them are maintained only by hand pollination. Two species of native lobeliads, *Brighamia insignis* and *B. rockii* (Shepherd et al., 2003), are examples whose principal sphingid moth pollinator is believed to be extinct (Kearns et al., 1998). In other cases, broadly applied insecticides have killed some native pollinators, resulting in low seed production in two species of wild plant (Thomson et al., 1985).

A more subtle form of pollinator limitation occurs when a plant species loses its pollinators to competition with other plants that have overlapping flowering seasons and share the same habitat (Kephart, 2005). Pollinators often prefer one plant species over another because of differences in floral

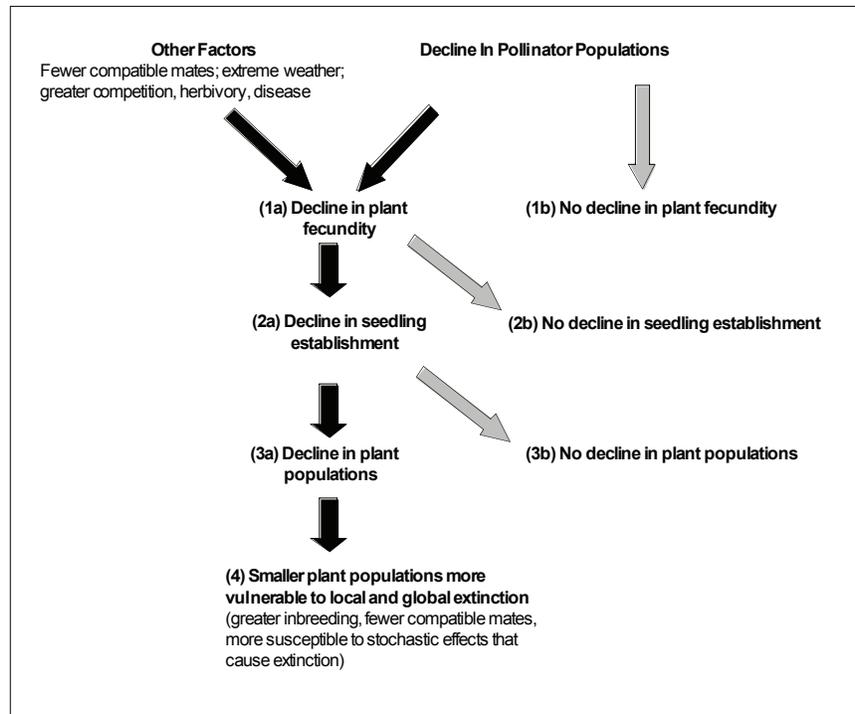


FIGURE 4-4 Possible effects of declining pollinator populations and other factors on the abundance and persistence of plant species. Effects represented by black arrows are cause for concern because they could lead to local or global extinctions.

rewards that can be collected in a given foraging period (Bernhardt, 1984). Plant fecundity is reduced when pollinators forage elsewhere and do not deliver enough conspecific compatible pollen to recipient plants (Campbell and Motten, 1985; Waser, 1978). Thus, competition for pollinators can depress plant fecundity—even when pollinators are locally common—because of the effects of plant community composition on pollinator behavior. In some plant species, no floral rewards are provided to pollinators and the flowers are thought to mimic rewarding flowers of other species or females of pollinating insects, whose males attempt copulation (Proctor et al., 1996) (Chapter 2). Such “deceptive” species could be especially prone to pollinator limitation because some pollinator species could learn to avoid them. For example, orchid species with flowers that lack food or chemical rewards for pollinators often exhibit very low fruit set, a condition commonly attributed to pollinator limitation (van der Cingel, 2001).

BOX 4-2

Pollen Supplementation Experiments

Seed production is influenced by the supply of resources available to the plant for producing reproductive structures as well as by the availability of compatible pollen for siring seeds. A common way to test for pollen-limited fecundity (seed set) is to carry out pollen supplementation experiments (Ashman et al., 2004). The flowers of one set of plants are hand-pollinated with ample amounts of compatible pollen, and their seed set is compared with that of flowers on naturally pollinated control plants (Kearns and Inouye, 1993; Thompson, 2001). Thorough hand-pollination of all of a plant's flowers throughout its lifetime can aid in differentiating between resource limitation and pollen limitation (Zimmerman and Pyke, 1988) in that resource limitation might prevent plants from producing fruits in successive years even when there is no shortage of pollination.

Hand-pollination is impractical, however, in long-lived or many-flowered species like shrubs and trees. If only a fraction of the plant's flowers are hand-pollinated, a separate set of control flowers should be used to determine whether artificially high seed set from hand-pollinated flowers causes artificially low seed set on the remaining, naturally pollinated flowers. Such an outcome could result because resources that are used early in the growing season are not available for later fruit set (Knight et al., 2005a; Stephenson, 1981).

Similarly, to avoid overestimating the extent of pollen limitation, investigators should determine whether artificially high fecundity in one year is followed by lower fecundity or reduced vegetative growth in the next year, as occurred in moth-pollinated crane-fly orchids (*Tipularia discolor*) in Maryland (Snow and Whigham, 1989). Pollen supplementation experiments should be carried out in several populations, including small, isolated populations, to account for temporal and spatial variation in pollinator service. Some studies probably over- or underestimate the extent of pollen limitation, but meta-analyses of pollen supplementation experiments can correct for many of these shortcomings (Knight et al., 2006). Careful experimentation can reveal the relative contributions of resource limitation and pollen limitation within a single species (Asikainen and Mutikainen, 2005; Campbell and Halama, 1993).

Because several mechanisms can account for low fecundity (Figure 4-4), it is useful to distinguish between two types of pollen-related constraints on seed production: *pollinator* limitation (insufficient pollinator service) and *pollen* limitation (insufficient delivery of compatible pollen to receptive stigmas; see Thompson, 2001). Low numbers of pollinators often cause pollen

limitation of seed production, but not all examples of pollen limitation result from low numbers of pollinators. For example, pollen limitation can occur in self-incompatible species that are highly clonal (Duncan et al., 2004), in populations without compatible mating types (Demauro, 1993), or during mass flowering (Vance et al., 2004) even when pollinators are common because too little outcross pollen is delivered to receptive stigmas. Methods for quantifying pollen limitation of seed set are described in Box 4-2. Plant populations that experience chronic and increasingly severe symptoms of pollen limitation are prime candidates for further study to determine whether low fecundity can be attributed to declining pollinator populations.

Several recent reviews indicate that pollen-limited fecundity is widespread in natural populations and can be severe (Burd, 1994; Knight et al., 2006; Larson and Barrett, 2000). Burd (1994) reported that 62 percent of 258 species exhibited pollen limitation at some sites and times, and Ashman and colleagues (2004) found evidence for pollen limitation in 62 of 85 cases in which hand-pollination was carried out on whole plants. In agreement with previous surveys, Knight and colleagues (2005a) reported that pollen limitation was more common in self-incompatible species than in self-compatible ones, and plants with fewer pollinator species were more likely to be pollen-limited than were those with many. Vamosi and colleagues (2006) reported a strong positive correlation between plant species richness and pollen limitation on a global scale, but there was no clear explanation for this association. The investigators hypothesized that competition for pollinators is more prevalent in species-rich communities, but they were unable to determine whether competition for pollinators is a natural and long-standing phenomenon or whether lower fecundity is a consequence of recent declines in pollinator populations.

In general, little is known about whether pollen limitation of seed set in wild plants has become more chronic or more severe on a large scale in recent decades. In any given species, the ratio of flowering plants to foraging pollinators can vary greatly during the flowering season, among locations, and over time (Fenster and Dudash, 2001), so it is difficult to identify all but the most drastic pollinator shortages. Despite that, well-planned pollen supplementation experiments can provide useful tests for pollinator service. They also are more manageable than tracking pollinator population trends directly or attempting to correlate variations in pollinator abundance with plant fecundity. Pollen supplementation experiments provide information about the immediate consequences of pollinator shortages, especially when studies include flower-bagging treatments that completely exclude pollinators. Conservation biologists use hand-pollination to determine whether insufficient pollination might contribute to the decline of threatened and endangered species, although that often is not the case (Bigger, 1999; Johnson et al., 2004; Rasmussen and Kollmann, 2004). Long-term monitoring of

pollen-limited fecundity (Chapter 5) is a prerequisite for securing compelling evidence of the functional consequences of pollinator declines.

Direct and Indirect Effects of Pollinator Shifts

Specialization and Redundancy in Plant-Pollinator Interactions

Pollination is typically a mutualistic relationship, and disrupting it can have immediate and significant consequences—at least for the partners directly involved—although the consequences might not be easily or immediately discerned. Janzen (1974) and Kevan (1974) suggested that loss of mutualisms could be an insidious process that might go unnoticed but that eventually would have major consequences for the integrity of an ecosystem. The complex nature of many plant-pollinator relationships, which can involve many links among species, could mean that the loss of component species would eventually elicit a sequence of plant or pollinator extinctions (Memmot et al., 2004; Olesen and Jain, 1994; Rathcke and Jules, 1993). Few studies have investigated how the breakdown of mutualistic pollination relationships might contribute to the decline of endangered plants (Robertson et al., 1999), but there are examples of the extinction of the primary pollinators of some species (Cox and Elmqvist, 2000; Ladley and Kelly, 1995; Robertson et al., 1999; Weller, 1994). Memmot et al. (2004) used records of flowers and pollinators to simulate the consequences of progressive pollinator extinction by removing pollinator species and observing which plants were left without pollinators as a result. In the simulations, the proportion of plants visited by pollinators declined differentially depending on whether pollinators are removed at random, systematically from least specialized (generalist) to most specialized, or systematically from most specialized to least specialized. The percentage of plants visited decreases more or less linearly if generalist pollinators are removed first. If the pollinators are removed in random order or in the order from least to most specialized, the percentage of plants visited decreases in a steadily accelerating pattern. These results suggest that loss of generalist pollinators pose the biggest threat to pollination systems (Memmott et al., 2004).

Pollen limitation of fruit or seed set can serve as a useful indication of pollinator decline. However, although many researchers have demonstrated apparent pollen limitation, few have investigated its effects on the demographics of plant species (but see Johnson et al., 2004; Ward and Johnson, 2005). The decline or loss of specialist pollinators would appear to be an obvious case in which to find consequences for conservation. Steiner and Whitehead (1996) identified a case in which the floral form of a South African shrub (*Ixianthes retzioides*) suggested that a large oil-collecting bee was the coevolved pollinator, although no such bee could be found in the popula-

tions examined. The minimal seed set that occurs in the populations appears to be the result of visits by pollen-collecting bees. There are other cases in which the loss of a coevolved pollinator appears to have been ameliorated by the arrival of introduced species that visit and pollinate the flowers. For example, in Hawaii the Japanese white-eye *Zosterops japonicus* has taken over the role of extinct or rare native birds in pollinating at least two plant species (Cox, 1983; Lammers et al., 1987). Plants with long, curved corollas, which might have depended on pollinators with matching mouthparts, have had unusually high extinction rates on Pacific islands; these losses have been accompanied (or preceded) by extinctions of their pollinating birds (Pimm et al., 1994).

Although few North American plant species rely on a small number of pollinator species for seed production, many plants depend heavily on specific floral visitors, such as bumble bees, for effective pollination. Plants have evolved suites of floral traits that attract and reward pollinators and pollinators can be classified into functional groups based on the types of flowers they pollinate (reviewed by Fenster et al., 2004).

To explore the extent of specialization for pollinators, Fenster and colleagues (2004) examined visitation data for 278 animal-pollinated plant species in Illinois that had been studied almost 80 years earlier by Robertson (1929). Recognizing that not all floral visitors are effective as pollinators, Fenster's group reported that 75 percent of the plant species were visited mainly by species in only one or two of nine functional groups (long-tongued bees, short-tongued bees, other Hymenoptera, Diptera, Coleoptera, Lepidoptera, Hemiptera, Neuroptera, and birds). In contrast, Waser and colleagues (1996) examined Robertson's (1929) records and noted that 91 percent of 375 native plant taxa reported in that study had been visited by more than one pollinator species. These reviews suggest that flowers of many plant species are visited by generalist pollinators as well as by pollinators in particular functional groups (Tudor et al., 2004).

If pollinator declines occur differentially in different taxonomic groups, rather than across all categories of major pollinators equally and simultaneously, the consequences for plant reproduction depend on the degree of redundancy in pollinator communities and on changes in the composition of pollinator communities. Redundancy has been described for a variety of plant-pollinator relationships; angiosperms in general could thus be buffered against losses of individual pollinator species (Waser and Ollerton, 2006). Most pollinators visit a variety of plants, and many plants are attractive to a range of pollinators (Memmott, 1999; Memmott et al., 2004). Because most pollinators are not completely constant to particular flowers, plant-pollinator interactions represent a complex web. Redundancy is one characteristic of community-level analysis of plant-pollinator relationships in general (Memmott, 1999).

The importance of redundancy among co-occurring pollinators is apparent in the variation in floral availability among locations, over time (for example, Saavedra et al., 2003), and among pollinators. The redundancy of services is a safety net for the long-term survival of plants and pollinators alike. Sharing of pollinators also can facilitate interactions among plants (Moeller, 2004). An example of the dynamic nature of pollinator communities involves the creosote bush, *Larrea tridentata*, a plant visited and pollinated by many specialist bees in the southwestern United States and Mexico. There are few long-term studies of bee abundance and diversity, but one investigation in undisturbed sites revealed that only a minority of abundant bee species was typically persistent, even after 20 years (Cane et al., 2006). Most of the bee species in the *Larrea* pollinator guild were uncommon, geographically sporadic, and temporally unpredictable (Cane et al., 2006). Williams and colleagues (2001) surveyed published studies and reported that bee faunas are typically locally diverse, highly variable in space and time, and often rich in rare species. These attributes of pollinator guilds indicate that intense long-term sampling among sites is necessary to differentiate the changes that are attributable to specific impacts of pollinator declines from the natural dynamics of populations and communities. These attributes also suggest that a metapopulation model that accounts for local disappearance and reintroduction of insect populations may be typical of many pollinator species. Because plant-pollinator interactions are highly connected and plant and pollinator populations can shift in time and space, conserving mutualisms might require a better understanding of their population dynamics and interactions.

Pollinator Declines, Plant Demography, and Genetics

The degree to which declining pollinator abundance affects plant population dynamics depends on several factors (Harris and Johnson, 2004), as illustrated in Figure 4-4. First, a decline in pollinators will not necessarily result in lower seed production (step 1, Figure 4-4). The prevalence of pollen-limited fecundity (Knight et al., 2006) suggests that low seed set or fruit production could be exacerbated by declining pollinator populations, but that might not be the case if alternative pollinators are present or if the plant is autogamous (self-pollinating) when pollinators are absent. Even when seed set remains high, though, increased rates of selfing could lead to poor seed quality because of inbreeding depression (Charlesworth and Charlesworth, 1987). In species that typically outcross, the survival and reproduction of selfed progeny are often lower than they are for outcrossed progeny (Dudash, 1990). Plants with mixed mating systems could be forced to increase reliance on selfing instead of outcrossing for seed production (Goodwillie, 2000).

The second condition that must be met for population-level responses to pollinator declines is for lower seed production to translate into lower seedling establishment (step 2, Figure 4-4). If seedling establishment is limited by some factor other than seed production, such as dispersal, seed predation, germination microsites, or high seedling mortality, then reduced fecundity might not affect seedling recruitment. Few studies have demonstrated that plant population size is seed-limited (Brys et al., 2004; Juenger and Bergelson, 2000). Empirical study of seed limitation is challenging. Vast numbers of seeds never reach a suitable site for seedling establishment, which is often patchy and episodic, and the effects of small but chronic decreases in plant fecundity on seedling populations could be difficult to measure in the field. Therefore, plant population ecologists often rely on population modeling based on empirically derived transition probabilities to predict the effects of reduced or enhanced fecundity on seedling establishment (Miriti et al., 2001).

The third condition that must be met for population-level responses to pollinator declines is for decreased seedling establishment to cause decreases in the number of mature plants. As with seedlings, the survival of young plants to sexual maturity can be strongly limited by competition, herbivory, extreme weather, human activity, and numerous other factors. Population modeling is useful for determining how this stage of the plant's life history affects the number of mature plants. Drastic reductions in recruitment could be detectable in natural populations, and small, undetectable effects of declining fecundity could be insignificant or important. If the plants are long-lived perennials, it might be many years for the loss of pollinator services to become apparent in the population structure. Many wild plant populations already are declining because of habitat loss, competition with invasive species, overgrazing by livestock or deer, and other factors (Ellstrand and Elam, 1993); more information is needed to ascertain whether declining pollinators could induce or exacerbate the loss of plant populations. Such a decline in wild plant populations because of pollination deficits might be in progress, but there is a dearth of published evidence for its occurrence in North America during recent decades.

If all the consequences of declining pollinator populations in fact occur (which seems unlikely), plant populations could become more vulnerable to an extinction vortex. The extinction vortex refers to the interacting factors that serve to reduce small populations progressively because of the increased risk of demographic and genetic consequences of small population size, including genetic erosion, inbreeding depression, decreased reproductive success, and greater susceptibility to catastrophes and random variations in environmental parameters (Kearns et al., 1998). One demographic risk is the Allee effect (inverse density dependence at low densities), which has

been demonstrated experimentally in plant populations (Groom, 1998; Hackney and McGraw, 2001) and observed in nature (Lamont et al., 1993). If there are no compensatory mechanisms for pollinator loss, and if reduced seed production from pollinator loss is directly reflected in smaller plant populations, these populations could enter an extinction vortex (Bond, 1994). Only careful research can disclose the necessary information about breeding systems, specificity and redundancy of pollinators, and plant life histories that will allow accurate prediction of the consequences of pollinator declines or losses.

At the other end of the spectrum, pollinator populations could increase and have a positive effect on plant abundance. One such case involves banyan trees, introduced ornamental fig species (especially *Ficus benghalensis*, *F. altissima*, and *F. microcarpa*) that became invasive pests in southern Florida subsequent to the inadvertent introduction about 25 years ago of the nonnative wasps that pollinate them (Nadel et al., 1992).

Indirect Effects of Pollinator Declines

There is a possibility that a cascade of ecological consequences could follow from the loss (or change in abundance) of roots, stems, leaves, flowers, fruits, and seeds—all of which can be resources for herbivores (including seed predators)—produced by plants. A broad range of herbivores and frugivores is supported by such resources, as are parasites and parasitoids of those species. Decreases in seeds, nuts, and fruits could be damaging to many species of insects, birds, and mammals, even if plant populations do not exhibit declines. More severe effects are expected if populations of mature plants become scarcer. For example, trophic cascades and the loss of shelter and nesting sites associated with plant species decline could cause reductions in bird populations. An example of how pollination itself can be part of a trophic cascade is provided by a study of the effects of fish as predators of dragonfly larvae in Florida (Knight et al., 2005b). Adult dragonflies are predators of some pollinators, so plants near ponds with dragonfly-eating fish receive more pollinator visits and are less pollen-limited than are those near fish-free ponds. This example suggests that pollinators are an important food resource for insectivorous predators.

Economic and Financial Consequences

Major shifts in natural pollinator populations could have economic repercussions either directly—in their appeal to nature lovers and collectors—or indirectly in their effects on the plants they pollinate. Some pollinators are appreciated aesthetically; butterflies and hummingbirds are

prime examples. That the honey bee is the state insect of 17 states and that various butterflies are state insects in 23 additional states (http://www.netstate.com/states/tables/state_insects.htm) is an indication of the visibility of pollinating species and the value placed on them. Apart from their intrinsic value, pollinators generate economic benefit through tourism. In 2000–2001, about 250,000 tourists visited the monarch butterfly reserve in west-central Mexico (Barkin, 2003). Colorado, Florida, Costa Rica, and Brazil host butterfly and bird tours (<http://wingsbirds.com/birdsand.htm>), although no estimates are readily available on total tourist expenditures at these sites.

Apart from ecotourism, at least one study shows evidence of park visitors' expressed willingness to pay to protect endangered butterfly species (of *Boloria aquilonaris* in Germany; Degenhardt and Gronemann, 1998). The existence of various pollinator conservation groups also provides evidence of people's willingness to pay to ensure the survival of endangered butterflies and birds. Examples include the British and Dutch Butterfly Conservation organizations (<http://www.butterfly-conservation.org/> and <http://www.vlinderstichting.nl/>), the American Butterfly Conservation Initiative (<http://www.butterflyrecovery.org/>), the Xerces Society (www.xerces.org), and the Hummingbird Society (<http://www.hummingbirdsociety.org/>).

The loss of major groups of pollinators in natural areas could trigger changes in abundance or community composition, or even the loss of plant species that depend on pollinators for sexual propagation. The economic value of such losses stems from two sources. The first is the combination of existence, bequest, and cultural values that some people would be willing to pay to ensure species survival, enjoyment, or use by future generations. Also important are the aesthetic benefits or cultural satisfaction of watching pollinators at work. This broad category of value applies not only to the pollinator species, but also to plant species that depend on them for reproduction and to animal species that depend on associated fruits and seeds for food. No studies appear to have estimated willingness to pay to prevent such wild species losses that would attend pollinator decline.

The second source of economic value is the value of losing the potential opportunity to generate future income, for example by commercial pharmaceutical discoveries that could have come from a species that will be lost. The "bioprospecting" literature has attempted to estimate the value of conserving biodiversity hotspots. Published results ascribe low values to land conservation, except in areas with very high biodiversity, because the probability of finding commercially exploitable species is low (Rausser and Small, 2000; Simpson et al., 1996). Theoretical valuations from models of complex species interaction offer less definitive results (Simpson, 2002) but give no guidance for small-scale biodiversity loss attributable to pollinator shifts. Extrapolating from these findings, the likely value of the small

number of plant species that might be lost as a result of reproductive failure that is caused by a loss of pollinators is likely to be small. Finally, some economically important wild species (for example, ginseng) that suffer from pollinator limitation also are severely threatened by other stressors, such as overharvesting and deer grazing (McGraw and Furedi, 2005). In such cases, species demise is only partially attributable to pollinator limitation.

CONCLUSIONS

Severe shortages of pollinators could cause many common food crops to become more expensive and perhaps less available, but there is no strong evidence for a current pollination crisis in agricultural production in North America. Most animal-pollinated crops can be serviced by honey bees, and farmers are accustomed to paying more for these services when necessary. Chronic pollinator shortages should lead to market adjustments and other innovations, although the demand for supplemental pollination has been strong recently, especially among California's almond growers. Importing managed pollinators from other countries or regions can lead to the introduction and spread of pathogens and unwanted bee species (Chapter 3). Therefore, it is prudent to sustain wild-pollinator populations as a means of buffering current and future shortages of managed pollinators of agricultural crops. In some cases, farmers could find that promoting wild pollinators that can supplement or substitute for managed pollinators could provide greater yields than will complete dependence on rented honey bee colonies (for example, Greenleaf, 2005). Intensive agricultural practices and pesticide use can reduce wild-pollinator diversity and abundance (for example, Kevan, 1975b; Kremen et al., 2002b; Larsen et al., 2005). Strategies for promoting abundance of wild pollinators are presented in Chapter 6.

In natural areas, the consequences of pollinator shifts on ecosystem services and possible solutions to these problems are varied and complex. Relatively few plant species rely on a single pollinator species or even on a single category of pollinators for reproduction. Because of the redundancy of most plant-pollinator communities, the ecological consequences of losing a small number of pollinator species could be limited. However, the loss of pollinator species reduces the redundancy of pollinator services in the ecosystem, and thus its resiliency, so that further losses of pollinator species would likely have more severe consequences for the ecosystem.

Plant communities in which massive pollinator declines are reported, for example because of persistent pesticide use or extensive habitat degradation, merit careful study of ramifying consequences for biodiversity. The ecological consequences of widespread pollinator declines could be substantial, but they could be difficult to detect because seed production varies dramatically in response to many biotic and abiotic factors (Figure 4-4). Moreover, the

effects of sustained declines in seed production on the size and abundance of plant populations could be subtle, slow processes that are real and overlooked by short-term studies. There is little available evidence to suggest that recent pollinator declines in North America have resulted in smaller populations of wild plants, possibly because the challenges of obtaining evidence are formidable. More research is needed to assess ecological consequences of current and future pollinator declines.

5

Monitoring Pollinator Populations and Services

Given that information on the status of pollinators and pollination services is far from complete, it is important to establish standardized, wide-scale, long-term protocols for monitoring pollinator populations and pollination services so that future changes can be assessed and appropriate actions taken. Existing monitoring efforts, in place for commercial honey bees and for some wild bee, butterfly, bird, and bat pollinators, provide a starting point. However, all extant programs need to be improved and an overarching framework will be useful for establishing cost-effective and feasible monitoring programs for a broader range of commercial and wild pollinators and pollination services in North America.

REVIEW AND ASSESSMENT OF CURRENT MONITORING PROGRAMS

Commercial Honey Bee Colonies

The National Agricultural Statistics Service (NASS) generates agricultural production statistics through the use of annual surveys of producers of agricultural products in each state. NASS offices continuously update producer lists, which are solicited from a variety of sources including commodity and grower groups. Beekeeping is one of the industry groups monitored by NASS. NASS reports on beekeeping operations through its annual honey report and its 5-yearly agricultural census.

The NASS Annual Honey Report of beekeeping commodities includes

national statistics on the price of honey (per pound) by color and marketing channel, and the following commodity statistics for each state:

- The number of honey-producing colonies.
- The average honey yield per colony.
- Total honey production.
- The average price per pound paid to beekeepers.
- Total value of honey production.
- Stocks of honey held by producers (not including stocks held by producers under the commodity loan program).

Data from states with few beekeeping operations—Connecticut, Delaware, Maryland, Massachusetts, New Hampshire, Oklahoma, Rhode Island, and South Carolina—are pooled to maintain confidentiality. Colony counts reported by NASS in its Annual Honey Report are based on beekeepers with more than five colonies and on honey-producing colonies only. Colony counts include all honey-producing colonies in a state and may count colonies more than once if they produce honey in more than one state (migratory beekeeping).

The 5-yearly Census of Agriculture uses different counting procedures than the Annual Honey Report. The most recent 2002 census (USDA-NASS, 2004a) counted all bee colonies, and counted them only “in the county where the owner of the colonies largest value of agricultural products was raised or produced” (USDA-NASS, 2004a, Appendix A, p. A-8). The census reports inventories and sales of colonies of bees, and honey produced, both nationally and by state.

The data reported suffer from a number of ambiguities. Restricting reported counts to honey-producing colonies results in an underestimate of the number of colonies; although NASS collects data in its annual survey form “Bee and Honey Inquiry” on the total number of colonies, they report on only the honey-producing colonies. According to the most recent agricultural census, for example, 30 percent of the nation’s 17,357 beekeeping operations did not produce honey in 2002 (USDA-NASS, 2004a, Table 2.19, p. 378). Yet counting colonies in each state in which they produce honey results in an overestimate of the number of colonies. The magnitude of these two countervailing errors is undetermined. Restricting colony counts to beekeepers with more than five colonies also results in an underestimate of the number of colonies nationwide. This undercount may involve as many as 100,000–400,000 colonies, assuming 100,000 hobbyist beekeepers with 1–4 colonies each (Chapter 1). Although, the colonies of most hobbyists are unlikely to find their way into the commercial pollination marketplace, they may contribute substantially to pollination for small grower operations, backyard gardens and urban landscapes, and wild (native and weedy) plants.

NASS statistics also do not include an assessment of pollination-relevant characteristics such as colony quality (strength, presence of parasites or pathogens), number of colonies lost over the winter (trade journal reports of winter losses are largely anecdotal), number of colonies rented for pollination, pollination rental fees, crops pollinated, and the numbers of queens and packages produced. At present, NASS statistics provide data only from beekeepers; such information from growers as rental price paid or the ease of obtaining the appropriate pollination service would provide a useful comparison with data collected from beekeepers to allow for an assessment of demand and shortages.

Wild Pollinators

Bees

Repeat Surveys

Several contemporary investigators have visited historical field sites where earlier pollinator surveys, particularly of native bees, had been conducted to determine if landscape changes during intervening years had resulted in changes in bee guild composition or losses of species from the area. Carlinville, Illinois, was sampled from 1884 to 1916 by Robertson (1929), who collected 214 bee species on over 400 plant species. Of the 214 species, 157 were found on only 24 of the plant species sampled. Approximately three-quarters of a century later (1970–1972), Marlin and LaBerge (2001) repeated that survey in Carlinville, concentrating their sampling effort on the 24 plant species that provided the bulk of the bee species reported by Robertson (1929). They collected 140 species of bees representing 82 percent of the species found by Robertson (as well as 14 species not recorded on those plants in the earlier survey). The relatively high degree of similarity in the bee community, despite the passage of 75 years and extensive landscape changes, was not the anticipated result. The authors suggested that patches of diverse habitats embedded within the agricultural matrix (for example, rural grasslands, forests, and open woods) have maintained bee diversity over time despite major changes in land use patterns.

Kevan and his colleagues have been analyzing data for pollinator diversity and abundance (Kevan et al., 1997) on New Brunswick blueberry fields for a period of about 8 years and find that the Sørensen, and other indices, of similarity between years but on the same fields are typically low (about 0.2) (unpublished). Turnock et al. (in preparation) have analyzed 8-year-long patterns of abundance in bumble bees in Manitoba, and noted changes by orders of magnitude from one year to the next. Javorek has some longer term studies ongoing in New Brunswick and Nova Scotia (Javorek et al., 2002). Sheffield (2006) has compared the data of Brittain (1933)

with his own and found that by and large, the diversity of bees that visit apple blossoms has not changed. Roubik studied euglossine bees at chemical baits for 20 years in Panama and reviewed other monitoring studies of bees conducted in California and in Central and South America (Roubik 2001). The euglossine bee guild in Panama showed no detectable overall change in species richness over 20 years, but interannual variability in bee abundances, both at the community and species level, was high (4–14 fold, respectively). He concluded that surveys must include a minimum of four sampling years to detect statistically significant trends in bee populations (Roubik, 2001).

New Monitoring Programs

Several of the most comprehensive and extensive long-term monitoring programs for bees have been established outside temperate North America (for example, Europe, Box 5-1). In recent years, however, several notable programs have been initiated for monitoring North American bee species. Since 2002, James Cane (U.S. Department of Agriculture's Bee Biology and Systematics Laboratory in Logan, Utah) has coordinated a network of professional scientists collecting data on the diversity and abundance of bees at native and cultivated squash and gourd plants in Canada, the United States, and Mexico using standardized observation and sampling techniques (<http://www.ars.usda.gov/Research/docs.htm?docid=12040>). This effort is designed to establish baseline data and assess changes in cultivated squash and gourd bee guild populations over time and under different land management practices.

Butterflies

As with bees, many of the longest and most comprehensive monitoring programs for butterflies are conducted outside the United States, either in the New World tropics (for example, the 35-year program in the Atlantic Forest region, Brown and Freitas, 2000) or the 30-year Butterfly Monitoring Scheme in the United Kingdom (Roy et al., 2001). However, several U.S. butterfly species have been studied and their populations censused for decades by individual investigators. Perhaps best known are the long-standing studies of Paul Ehrlich and colleagues of *Euphydryas editha bayensis*, the Bay checkerspot butterfly. This species was regularly censused in Stanford University's Jasper Ridge Biological Preserve near Palo Alto, California, for almost 40 years (Ehrlich and Hanski, 2004; Chapter 2). Among the insights gained from this long-term study are the prevalence of local extinctions (even of federally protected species), the importance of topographic heterogeneity to allow populations to weather extreme droughts and floods,

and the need for nearby populations to provide migrants for recolonizing habitat patches following local extinctions. These insights apply not only to *Euphydryas editha bayensis* populations, but also to many other pollinator species that require habitat heterogeneity (particularly the ones that exist in subdivided populations because of habitat fragmentation). Habitat heterogeneity accommodates the different habitat requirements of larvae and adults and allows the insects to respond adaptively to intraannual and interannual weather variations.

Another notable butterfly monitoring effort, also in California, has been conducted near Davis, California. Arthur Shapiro and colleagues (University of California at Davis) conducted an annual census of butterflies from Willow Slough, California, for over 29 years. Examination of census records of over 39,000 individuals representing 36 species for trends in faunal diversity and in the probability of presence of individual species (Chapter 2 and O'Brien et al., forthcoming) revealed a statistically significant decline of 38 percent in overall species diversity. That long-term studies are needed to detect declines is evidenced by the fact that for 22 years the measured decline in observed richness did not achieve statistical significance.

The annual fall migration of the monarch butterfly, *Danaus plexippus*, has been monitored according to a standardized protocol by Lincoln Brower and colleagues on an annual basis from the peninsular town of Cape May, New Jersey, from 1991 to 2004 (Walton et al., 2005). The 13-year survey revealed substantial annual fluctuations in the numbers of migrating butterflies, with a 13-year low recorded in 2004. Across the 13-year period, numbers of monarchs counted per season varied 35-fold. In general, years of above-average abundance tend to be followed immediately by years of below-average abundance, a pattern that, again, emphasizes the value of multiyear long-term monitoring in order to avoid drawing inappropriate conclusions about pollinator status.

North American Butterfly Association

The North American Butterfly Association (NABA, <http://www.naba.org>) has about 5,000 members and is the largest group of individuals in North America (Canada, United States, and Mexico) interested in butterflies. The Xerces Society for the Invertebrate Conservation and subsequently NABA have conducted the annual Fourth of July Butterfly Counts across North America since 1975 (<http://biology.usgs.gov/s+t/noframe/f070.htm>; <http://www.naba.org/counts.html>). Results are posted on the Internet (<http://www.naba.org/pubs/countpub.html>) along with a checklist of North American butterflies (<http://www.naba.org/ftp/check2com.pdf>). For example, in 2004, a total of 467 counts were held in 48 U.S. states, 4 Canadian provinces, and 1 Mexican state. Each count represents compila-

BOX 5-1
A Model Monitoring Program for Pollinators from Europe (ALARM)^a

An extensive and innovative European Union (EU) scientific program for long-term monitoring of bees and other pollinators has begun within the multicountry framework of conservation farming practices. The Assessing Large-Scale Risks for Biodiversity with Tested Methods project (ALARM; <http://www.alarmproject.net>) started in 2004. ALARM is a consortium of 54 partners from academic institutions representing 26 countries, including 19 EU countries (Austria, Belgium, Czech Republic, Denmark, Estonia, Finland, France, Greece, Ireland, Italy, Lithuania, the Netherlands, Poland, Portugal, Romania, Slovenia, Spain, Sweden, and the United Kingdom), and Bulgaria, Romania, Israel, Switzerland, and three International Cooperation states. From 2004 to 2009, 16.7 million euros are budgeted for the project. ALARM aims to quantify the environmental risks to biodiversity, including pollinators, with standardized and repeatable sampling methodologies. ALARM has five modules: pollinator loss, climate change, invasive species, environmental chemicals, and socioeconomics. The pollinator module objectives are to (1) quantify distribution shifts in keystone pollinator groups across Europe; (2) measure the economic and biodiversity risks associated with the loss of pollination services in agricultural and natural habitats; (3) determine the relative importance of drivers of pollinator loss; (4) develop predictive models for pollinator loss and consequent risks to habitat, humans, and wildlife; and (5) create and maintain a knowledge database to underpin the sustainable conservation and management of pollinator species across Europe.

ALARM researchers have just concluded an extensive analysis of before-and-after data from 1980 repeat surveys of native bees and flower flies (family

tions of all butterflies observed at sites within a 15-mile-diameter circle by teams of citizen-scientist observers in a 1-day period. Comparisons of the NABA count results across years have proved useful in elucidating effects of habitat and weather changes on North American butterflies (Kocher and Williams, 2000).

Monarch Watch

Monarch Watch (<http://www.monarchwatch.org/>) is a University of Kansas Entomology Program founded in 1992 and dedicated to education, conservation, and research on monarch butterflies in North America. It engages citizen-scientists in large-scale research projects designed to reveal

Syrphidae) in the United Kingdom and the Netherlands (Biesmeijer et al., 2006; see Box 2-2 in Chapter 2). ALARM is also undertaking many repeat historical observations of EU pollinators by resampling previously well-studied locations. The aim is to fill current knowledge gaps with point estimates of changes across Europe in regions where large national data sets are unavailable.

The ALARM group is developing and testing standardized and repeatable methods for sampling pollinators in six European countries using 48 natural and agricultural sites. Methods tested in parallel include trap nests for bees, water-filled pan traps, netting at flowers along fixed transects, and counts at fixed observation plots. The final ALARM standardized methods “toolkit” is planned to be ready for distribution to other researchers by 2007. The ALARM project provides a model for a monitoring program that could be replicated in North America. North America contains many of the same biomes (tundra, boreal forest, temperate deciduous and coniferous forests, prairies or steppes, Mediterranean scrub) as Europe, with a few additions (desert, subtropical, and tropical forests). A monitoring project in North America could be more complex ecologically but a lot simpler administratively than the European program, which involves 26 countries. Canada already has an existing Ecological Monitoring and Assessment Network (<http://www.eman-rese.ca/eman/program/about.html>), which is a cooperative partnership of federal, provincial, and municipal governments; academic institutions; aboriginal communities and organizations; industry; environmental nongovernmental organizations; volunteer community groups; elementary and secondary schools; and other groups and individuals involved in ecological monitoring.

^aPresentation to the committee by S. Potts, University of Reading, on October 19, 2005.

valuable information about monarch butterfly biology and their annual migration to and from overwintering sites in the state of Michoacan west of Mexico City. Participants tag 30,000–100,000 butterflies each year during the fall migration, with a recovery rate of tagged butterflies in Mexico of 0.6 to 1.8 percent per year (which is considered high given the distance the monarch butterflies travel, the hazards of the migration, and the overall population size). This is one of the largest mark and recapture programs in operation. All tag recoveries are posted online (<http://www.monarchwatch.org/tagmig/recoveries.htm>). An estimated 100,000 people participate in Monarch Watch each year, including students from over 2,000 schools, and nature centers and other organizations in Canada, the United States, and Mexico. A conservation initiative known as “Monarch Waystations”

(<http://www.monarchwatch.org/ws/>) has encouraged the creation and registration of over 600 monarch habitats (with host and nectar plants) located at schools, nature centers, zoos, private homes, and businesses. Monarch Watch serves as a model for how to maintain a long-term outreach program that engages the public in scientific endeavors and conservation relevant to pollinators (Rogg et al., 1999; Taylor, 2000). Other citizen-scientist programs for Lepidoptera could benefit from adopting their tagging methods and incentives for study and reporting.

Birds

A number of different programs monitor hummingbird populations, but the results they provide are often inconsistent, in part due to different temporal and spatial scales of study as well as different methodologies used. The Breeding Bird Surveys (<http://www.mbr-pwrc.usgs.gov/bbs/bbs.html>) provide data and trends for many bird species, including eight hummingbirds. In the 105-year database of Audubon Society's Christmas Bird Counts (CBC; <http://audubon2.org/birds/cbc/hr/graph.html>), no species of hummingbird appears to be declining. However, December is not a good time of year to census migratory species of hummingbirds in Canada (none recorded) and their abundance is quite low in the United States at that time because they are in Mexico. The data for nonmigratory Anna's hummingbird are highly variable (probably reflecting in part growth of participation in the CBC) but show no indication of decline. Although the eBird citizen science project of the Cornell Laboratory of Ornithology does not yet provide population monitoring data, it is working toward this goal. In Mexico, a country-wide effort to document birds was launched in 2005, *AverAves* (<http://www.ebird.org/aVerAves/>). Despite existence of multiple programs, many species, including those that are endangered or threatened, are not monitored at all. For example, of the 45 endangered species, only a small number have ever been or are currently being monitored (Sibley, 2000).

In addition to these large-scale, long-term monitoring programs, several individual investigators have carried out long-term monitoring of rufous (*Selasphorus rufus*) and broad-tailed (*Selasphorus platycercus*) hummingbirds for decades in the western United States, Canada, and northern Mexico. These monitoring programs have elucidated details of the migratory patterns and population and breeding structure that would otherwise probably not have been discovered. For example, Calder (1987, 1992; Banks and Calder, 1989) found that the broad-tailed hummingbird is subdivided into two populations: one that migrates to spend the summer in the United States, breeding from May through July and molting in midwinter, and a resident population that remains in Mexico year-round, molting in May and June and breeding from September through December (Calder and

Calder, 1992). In contrast, in the rufous hummingbird, all individuals migrate north in the early spring across the Pacific coastal states and then diverge into two breeding groups: one in the Pacific Northwest and one in the northern Rockies. Additional studies restricted to local populations have been useful in elucidating ecology and natural history, but could potentially better inform management action if conducted at a larger scale. E. Santana (University of Guadalajara, Mexico, personal communication, December 2005) has monitored the abundance of several hummingbird species in the Manantlan Biosphere Reserve of western Mexico for 18 years and found nonuniform interannual changes between species, which suggest differential responses among species to habitat and other changes. Another regional study (Schondube et al., 2004) conducted between 1995 and 2001 indicated that the number of rufous hummingbirds has remained relatively stable in western Mexico.

Although bird populations are monitored, the monitoring is not necessarily conducted at the most informative spatial or temporal scales. Data on seasonal, spatial, and numerical fluctuations on hummingbirds and other flower-visiting birds could be collected across the three countries in North America. The United States can play a role in promoting collaborative efforts to monitor population trends, biological factors, and pollination services by those species under standardized protocols.

Bats

The monitoring of pollinating bats to date has been limited to two of the four threatened and endangered species. In fact, the inclusion of two migratory nectar-feeding species on the U.S. Endangered Species List (as endangered) and the Mexican list of species at risk (as threatened, both species) stimulated the monitoring and study of the lesser long-nosed bat (*Leptonycteris curasoae*) and the Mexican long-nosed bat (*L. nivalis*) (Medellín, 2003; Medellín et al., 2004). The intermittent monitoring so far has allowed a preliminary understanding of the status, ecology, and movements of migratory pollinating bats. These species continue to be monitored by the Program for Conservation of Mexican Bats (Medellín et al., 2004). In Arizona, a monitoring effort by the Arizona Game and Fish Department (2006) continues to produce important information (Krebbs et al., 2005). For example, simultaneous visits to all known roosts of the lesser long-nosed bat in Arizona and northern Sonora have been conducted for the past few years. The simultaneous counts constitute one of the most robust ongoing efforts to assess the status and population dynamics of this species. Bats congregate in their roosts so that counting them in roosts provides an accurate assessment of a large proportion of their total population.

Because of their habit of roosting in caves, identifying ecologically sig-

nificant caves for ongoing standardized monitoring is essential for assessing the status of bat populations. Documenting population size and evidence of reproduction is the most important priority, but dates of arrival at and departure from the roosts, diet composition, and other data are important to acquire in order to understand conservation needs (Medellín, 2003). Given the long-distance, international movements of those species, only monitoring at large scales of multiple colonies across the species' summer and winter ranges will provide the needed information. International collaborative efforts in monitoring and conservation practices are therefore critical for the benefit of those primarily migratory species.

REQUIREMENTS FOR ADEQUATE MONITORING OF POLLINATORS AND POLLINATION FUNCTION

Commercial Pollinators

An accurate assessment of commercially managed pollinator status and function is a fundamental antecedent to a rational decision-making process aimed at recommending allocation of private and public resources for management of commercial pollinator species. An accurate assessment requires an unambiguous determination of the number and type of commercial pollinating units available, the quality of those pollinating units (for example, health and strength), assessments of annual and seasonal losses, pollination fees or purchase prices, and the crops that are pollinated with each species. Complete and accurate data will permit statistical trend analyses of commercial pollinator status and function, and such analyses can provide stakeholders with a rational basis for action.

Specifically, monitoring activities could include an array of pollination-specific characteristics. Questions could be directed to both suppliers of pollination services (for example, solitary bee operations and bumble bee companies), and consumers of pollination services (for example, crop growers). Questions for suppliers could include queries regarding the number of pollination units rented or sold for pollination (by crop); in the case of honey bees, the number of times a colony was rented in a year; and rental fees or selling prices charged for pollinating units. For honey bees, data should be segregated according to the crop being pollinated. Data on annual colony losses and colony losses during the previous winter should also be collected. Questions for growers could include queries on whether pollination services were purchased during the previous seasons, the species involved (honey bees, bumble bees, solitary bees), the number of units purchased or rented, the price or rental fee paid, the crop grown, and some measure of the difficulty in obtaining the desired pollination services.

NASS is already collecting some pollination-specific data, but surveys

could be adjusted to acquire the information mentioned above. Moreover, monitoring methods could be adjusted to eliminate current ambiguities in the honey data report and data collection could be modified to include tracking of winter losses of honey bee colonies. Such information can provide a measure of volatility in colony numbers that is not captured by current methods.

Wild Pollinator Populations

Little is known about the status of most wild pollinators in North America, especially for wild populations of native bees, the dominant pollinators of flowering plants on wild or unmanaged lands (Chapter 3); in particular, there is seldom a historical baseline to which modern data can be compared. Two sampling strategies could be employed to compensate for the absence of relevant baseline data. First, existing historical data could be used in conjunction with recent survey data to conduct focused assessments of the status of pollinators in certain regions of North America. For example, given a set of bee species collected from a specific locality in Connecticut between 1900 and 1930, a re-survey can be conducted to determine how many of those species can still be detected (see Box 2-3; Biesmeijer et al., 2006). Second, a long-term annual monitoring program could be initiated expressly to establish a baseline for evaluating status of pollinators at different times in the future. Such monitoring, in contrast to an assessment that provides a “snapshot” in time, can both illuminate trends in species abundance and allow detection of relationships between changes in community composition and putative environmental causes of change (Kevan et al., 1997; Kremen, 1992; Kremen et al., 1993). Understanding such relationships is crucial for developing plans to mitigate environmental change and to manage for species persistence (Walters and Holling, 1990). Although such programs are difficult to set up and maintain, the European ALARM project (Box 5-1) provides an inspirational example of a pollinator monitoring program across many countries.

In addition to assessing and monitoring pollinator populations and communities, monitoring pollination function over time is important. The relationship between the presence, absence, or abundance of a given pollinator species and the pollination service that a particular plant species receives is complex (Bond, 1995; Memmott et al., 2004; Morris, 2003). Relationships between plants and their pollinators are most commonly generalized; that is, most plant species have several to many pollinating species as visitors, and most pollinator species visit and pollinate many different plant species (Chapter 2). In addition, asymmetric specialization, whereby specialist mutualists can interact with more generalized partners, appears to be common in pollinator-plant networks (Vázquez and Aizen,

2004). This asymmetry can reduce the vulnerability that specialist species face in relying on only one or a few mutualist partners. These studies suggest that quite a few pollinators could become locally or globally extinct with little impact on the plants that they pollinate. Most of the work done to date is theoretical and predicts potential impacts on plant species based on deleting pollinators from known webs of interactions, rather than on observing impacts on plants as communities of pollinators decline in richness and abundance (but see also Fontaine et al., 2006). Because the impact of a decline in abundance or extinction of pollinator species on ecosystems is unknown, monitoring pollination function is as important as monitoring pollinator abundances.

A two-part program to, first, assess the current status of wild pollinators in North America, and second, to establish a framework for long-term monitoring of pollinator populations and function over time (Figures 5-1A and 5-1B) is thus a laudable goal. A possible model for setting up an assessment and monitoring program is described below. An assessment program could capitalize on past survey work by targeting re-surveys in areas that were well sampled in the past and by mining museum collections and the literature for historical data that correspond to areas of ongoing, high-intensity sampling. A long-term monitoring program could maximize results obtained per dollar spent by integrating professional scientist monitoring activity with citizen-

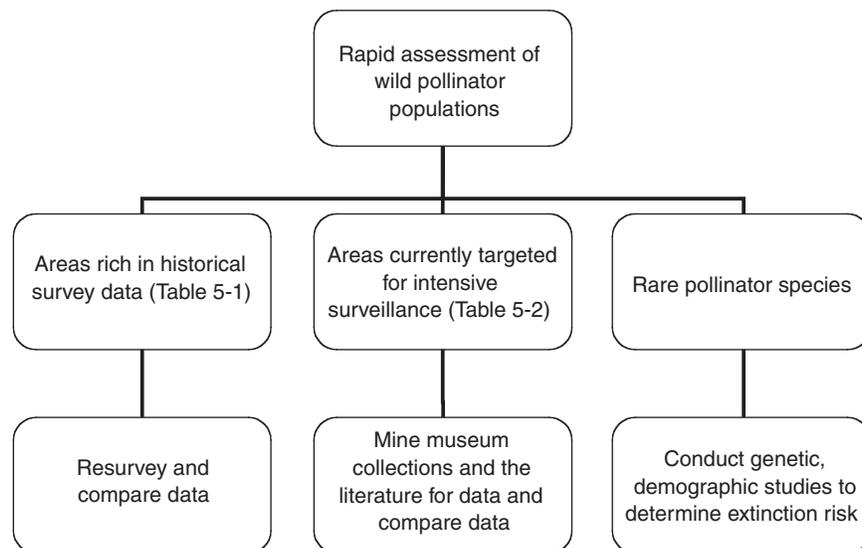


FIGURE 5-1A Assessment program.

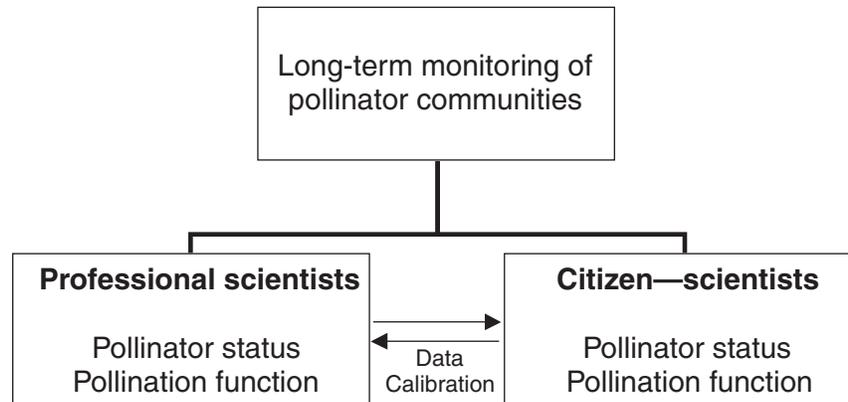


FIGURE 5-1B Monitoring program.

scientist monitoring activity in assessing both pollinator status and pollination function. Citizen-science monitoring programs are recent endeavors, and few have been subject to rigorous comparisons with professional monitoring. Figures 5-1 provide a flowchart illustrating the structure of each component of such an assessment and monitoring program.

With respect to carrying out this program, the professional science activities fall within the mandate of governmental agencies including the U.S. Department of Agriculture, the U.S. Geological Survey (USGS), the U.S. Fish and Wildlife Service, and the National Science Foundation's proposed National Ecological Observatory Network. The citizen-scientist activities could be coordinated, for example, by partnerships between nongovernmental organizations (NGOs), governmental organizations, and citizen groups. The North American Amphibian Monitoring Program (<http://www.pwrc.usgs.gov/naamp/>) provides a useful model. It is a collaborative effort among regional partners that include state natural resource agencies, nonprofit organizations, and USGS. Participating NGOs for a North American Pollination Monitoring Program could include the North American Pollinator Protection Campaign, the Xerces Society, Monarch Watch, and likely citizen-scientist groups such as native plant societies, gardening clubs, schools, friends of nature reserves, community farm alliances, or commodity groups. The Pollinator Watch Program in Canada is currently under development through the Environmental Monitoring and Assessment Network's Nature Watch Program (<http://www.eman-rese.ca/eman/naturewatch.html>).

Knowledge of all important pollinator taxa could benefit from monitoring programs. Funding restrictions might require prioritizing among taxonomic groups, at least initially. As arguably the most important and

least well-studied groups of pollinators (Proctor et al., 1996), wild bees could be a top priority for coordinated assessment. Lepidoptera, especially butterflies, have been utilized as a key indicator group for insects (for example, Fleishman et al., 2005) and their visibility, familiarity, and ecological importance argue for focusing monitoring efforts on this group initially, and then expanding to include others. That said, many of the monitoring techniques proposed here allow simultaneous collection of observations and samples of a wide range of flower-visiting species. Such data could be collected and archived even if time and resources do not allow processing and analysis immediately.

Assessment Program

Assessment programs will provide information about the status of a wide variety of pollinators in North America. The ALARM project showed that a before-and-after comparison based on past and recent surveys could reveal range contractions in many pollinator species (Biesmeijer et al., 2006; Box 2-3). The results suggest that concerns about pollinator status are warranted. Using that project as a guide, an assessment program in North America could include three activities:

- Conduct intensive field surveys to collect, curate, and identify insect pollinators, repeated over at least 3–4-year periods (because of year-to-year variability in populations and species composition; see Chapter 3), in regions where significant historical records (late 1800s to early 1900s for many localities in eastern North America; 1950s–1970s for more recently surveyed localities in western North America) are known to exist for pollinators (Table 5-1). Current species presence can be compared with historical records to determine the number of species that still occur in these geographic areas (Biesmeijer et al., 2006; Marlin and LaBerge, 2001).
- Capture historical data from museum collections (Anderson et al., 2002; Biesmeijer et al., 2006; Graham et al., 2004) for selected localities where intensive field surveys are currently being carried out for comparison of records. (See Table 5-2 for locations and sampling dates of recent or ongoing surveys.)
- Monitor populations of selected pollinator species that are rare or suspected to be in decline (for example, *Bombus* spp., Chapter 2), using contemporary genetic or demographic techniques. For example, for bees, recent studies suggest that measuring the proportion of diploid males (Chapter 3) may be a simple, but effective, genetic technique to determine whether populations have experienced significant decline and are at enhanced risk for the future (Roubik, 2003; Zayed and Packer, 2005; Zayed et al., 2004).

TABLE 5-1 Examples of Areas Appropriate for Repeat Survey of U.S. Pollinator Populations (Localities, Some of Which Have Been or Are Being Re-surveyed, Contain Substantial Collections of Bees and Other Flower-Loving Insects)

Locality	County	State	Collection Period	Collection Method
Portal	Cochise	AZ	1950–1970	Net
Antioch Dunes	Contra Costa	CA	1930–1960	Net
Mt. Diablo	Contra Costa	CA	1930–1950	Net
Surprise Canyon	Inyo	CA	1950–1970	Net
Altadena, La Crescenta	Los Angeles	CA	1930	Net
Tanbark Flat	Los Angeles	CA	1950	Net
Hastings Preserve	Monterrey	CA	1930–1940	Net
Sagehen Creek, Hobart Mills	Nevada	CA	1930–1960	Net
18 mi W Blythe	Riverside	CA	1950–1970	Net
Boyd Deep Canyon Desert Research Center	Riverside	CA	1940–1970	Net
Idyllwild, Keen Camp	Riverside	CA	1920–1940	Net
Palm Springs, Whitewater Canyon	Riverside	CA	1930–1960	Net
Riverside	Riverside	CA	1930–1950	Net
The Gavilan	Riverside	CA	1930–1950	Net
Morongo Valley	San Bernardino	CA	1930–1960	Net
Twentynine Palms	San Bernardino	CA	1930–1960	Net
Victorville, Apple Valley	San Bernardino	CA	1930–1960	Net
Borrego Valley	San Diego	CA	1930–1960	Net
Putah Creek and Canyon	Yolo	CA	1950–1960	Net
Moldenke transect, northern California		CA	1960–1970	Net
Boulder	Boulder	CO	1930–1940	Net
Rocky Mountain Biological Laboratory	Gunnison	CO	1975–1980s	Net
Miami and vicinity		FL	1930	Net
Moscow	Latah	ID	1930–1960	Net
Carlinville	Macoupin	IL	1890–1920	Net
Chicago and vicinity		IL	1920–1930	Net
Lawrence	Douglas	KS	1930–1960	Net
Plummer’s Island	Montgomery	MD		Net
Mount Desert and vicinity	Hancock	ME	1910–1950	Net
E.S. George Reserve	Livingston	MI	1970	Net
Hattiesburg	Forrest	MS	1940	Net
Raleigh	Wake	NC	1920–1950	Net
Fargo	Cass	ND	1910–1950	Net
Mesilla		NM	Early 1900s	Net
Rodeo	Hidalgo	NM	1950–1970	Net
Albany Pinebush Reserve	Albany	NY		Net
Ithaca and vicinity	Tompkins	NY	1880–1950	Net

continued

TABLE 5-1 Continued

Locality	County	State	Collection Period	Collection Method
Brooklyn (Flatbush, Prospect Park, Floyd Bennett Field)	Kings	NY	1890	Net
Gardiner's Island	Suffolk	NY	1910	Net
Corvallis	Benton	OR	1920–1960	Net
Curlew Valley	Box Elder, Oneida	UT, ID	1960–1970	Net, Malaise
Cache Valley	Cache, Franklin	UT, ID	1940–2000	Net, pan, Malaise
Milwaukee	Milwaukee	WI	1900–1930	Net
Laramie	Albany	WY	1970	Net

SOURCE: J. Asher, American Museum of Natural History, and T. Griswold, USDA, personal communication, October, 2005; Procter, 1946.

Monitoring Pollinator Communities and Pollination Function

A useful monitoring program must employ standardized, tested, repeatable methodology applied with sufficient spatial and temporal replication to ensure confidence and allow interpretation of time trends in the resulting data. Describing the many factors that must be taken into account in designing a monitoring program is beyond the scope of this report, but such factors are discussed by Elzinga et al. (2001) and Potts et al. (2005). Monitoring programs can be designed to assess specific techniques to guide management, or they can be designed to track trends over time to assess the changing status of species or ecosystems (Kevan et al., 1997; Kremen et al., 1993). The latter type of program is most appropriate for monitoring both pollinator communities and pollination function across large geographic regions such as North America.

Monitoring insect populations and their function as pollinators presents certain challenges. Many species can be identified only by a professional taxonomist or are not yet described so that the “taxonomic impediment” (Box 2-1) can be a significant obstacle (Kremen et al. 1993; O’Toole, 2002). In addition, insect populations tend to experience large interannual or interseasonal changes in abundance (Roubik, 2001; Wolda, 1988), making detection of temporal trends difficult. Insect communities often include many rare species (Magurran, 1988) and rare species are inherently less amenable to monitoring with confidence across space and time. Complicating the process of evaluating insect communities is that variation in composition can be extremely high, even in samples from nearby areas of the same habitat type, or at the same site across time (Williams et al., 2001). Thus, any monitoring program focusing on insect pollinators must address both the taxonomic impediment and the challenge of collecting data with sufficient spatial and temporal resolution to allow trend detection.

TABLE 5-2 Examples of Modern Inventory Areas for Bee Pollinators (Corresponding Museum Data Could Be Captured for the Listed Localities to Compare Between Historical and Modern Records and Provide a Status Assessment)

Location	State	Collection Period	Digitized	Records	Species	Data Owner ^a	Collection Method	Time Interval	Standard Interval	Plot	Notes
San Rafael Desert	UT	1979–1993	Yes	12,218	333	TG	Net		Biweekly		Biweekly on dunes
Death Valley National Park	CA	1993–1995, 1999–2000	Yes	7,065	270	TG	Net, pan		Biweekly		Trail segments systematically sampled
Pinnacles National Monument	CA	1996–1999	Yes	25,196	398	OM, TG	Net, pan		Biweekly		Identifications not complete
Clark County	NV	1998, 2004–2005	Yes	67,617	598	TG	Net, pan		Biweekly		Identifications not complete
Grand Staircase-Escalante National Monument	UT	2000–2003, 2005	Yes	99,156	647	OM, TG	Net	X	Biweekly	X	Identifications not completed for 2005
Dugway Proving Grounds	UT	2003–2004	Yes	6,783	223	TG	Net, pan	X	Biweekly	X	Identifications not completed for 2005
Yosemite National Park	CA	2004–2006	Yes	23,021		TG	Net, pan	X	Biweekly	X	Identifications not complete
Avalon Plantation	FL	1999–2000	Yes	3,000	125	SB	Net, pan		Monthly		
Yuma Proving Ground	AZ	2001–2002	Yes	5,000	>200	SB, U.S. Army	Pan		Monthly		
White Sands Missile Range	NM	2003–2005	Yes	10,000	>250	SB, U.S. Army	Pan		Monthly		

^aData owner: TG: T. Griswold, USDA-ARS; OM: O. Messinger, USDA-ARS; SB: S. Buchmann, University of Arizona, Tucson. SOURCE: T. Griswold, USDA-ARS, personal communication, October 2005.

A cost-effective approach to addressing the two kinds of obstacles to monitoring insect pollinators might be to involve both professional scientists and citizen-scientists in the effort (Lepczyk, 2005). The professional science component provides the scientific rigor and detail needed for robust assessments of biodiversity response to changes in management practices (Bednarek and Hart, 2005; Noss, 1990). The citizen-scientist component may then increase the temporal and spatial breadth of studies that can be conducted at minimal cost, but at a sacrifice of some quality in the data (Table 5-3). Studies conducted by citizen-scientists could be carried out at low taxonomic resolution (for example, “bumble bee,” “flower fly” rather than identifications at the genus or species level), thereby circumventing the difficulty in identifying most pollinating insects caught in field studies to the species level. Careful integration of citizen-scientist efforts with professional efforts (for example, calibrating the data collected by citizen-scientists against that from the professional scientist program—see below) is necessary to optimize the utility of the resulting data. An important added advantage to including citizen-scientists is that it builds appreciation and understand-

TABLE 5-3 Pollinator Long-Term Monitoring Program: Comparison of Professional and Citizen-Scientist Monitoring Programs

	Professional	Citizen-Scientist
Number of sites	50–100	Many
Type of sites	Gradients of disturbance and sites shared with citizen-scientist program	Many, of interest to citizens
Taxonomic resolution	High: genus and species	Low: operational taxonomic units such as bumble bee, sweat bee, flower fly
Temporal resolution	High: monthly, biweekly, or daily	Low: often annual
Pollinator status measurement	Species richness, relative abundance, identity (specimens)	Counts of operational taxonomic units (observations)
Pollinator function measurement	Pollen limitation for plants with varied breeding systems, including species studied by citizen-scientists	Fruit or seed set for self-incompatible plants; bulbil counts on agaves in Mexico
Goals	<ul style="list-style-type: none"> • Higher resolution of data along land use change gradients • Calibration of citizen-scientists’ data 	<ul style="list-style-type: none"> • Data from more sites than professionals could survey alone • Public involvement in pollinator monitoring, conservation
Benefits, costs, and caveats	Provides high-quality data but at high cost	Provides large quantity of data at low cost but must be tested, calibrated

ing of pollinators among stakeholders (for example, Condon, 1995; Kevan, 1975a). Examples of successful citizen-scientist monitoring programs that have yielded scientifically valid monitoring data with potential to assist in conservation and management of various species include the Tucson Bird Count (Turner, 2003; Turner et al., 2004), the Breeding Bird Survey (Mineau et al., 2005; Vance et al., 2003), and the House Finch Disease Survey (<http://www.birds.cornell.edu/hofi/>) of the Cornell Ornithological Laboratory (Altizer et al., 2004; Dhondt et al., 2005).

Professional Science Programs

The professional science program could be designed with two goals in mind: (1) to obtain an intensive, detailed data set to use in determining the long-term effect of land use change (the dominant force enhancing extinction rates and altering ecosystem processes; Millennium Ecosystem Assessment, 2005) on pollinator communities and pollination function, and (2) to obtain targeted data for a small number of sites with the goal of calibrating the data from the citizen-scientist programs to make the data from those programs more useful.

To assess the influence of land use change on pollinator communities, the professional scientist monitoring program could also monitor sites across an existing land use gradient, from relatively pristine natural habitats to extensively anthropogenically altered habitats. Studies across environmental gradients provide immediate information about the effects of land use change. They trade spatial coverage for (see also Greenleaf and Kremen, 2006a,b) time coverage by providing an estimate of the correlation between the accumulated environmental characteristics associated with different degrees of land use change and the community or functional characteristics. For example, Kremen et al. (2002b) found that the intensification of agriculture in California, from small-scale organic farms near natural habitats to large-scale conventional farms isolated from natural habitats, greatly reduced the diversity and abundance of wild pollinators at watermelon and other crops, and hence the services provided. In the intensively farmed region, many common species known from historical records have disappeared (Kremen et al., 2002b; Larsen et al., 2005). Thus a “snapshot study” can provide a useful amount of information about the local status of pollinator species (see also Kevan, 1975a; Kevan et al., 1997; Scott-Dupree and Winston, 1987).

Land use change is dynamic; for example, in the United States, European colonization was accompanied by extensive conversion of forested lands to agriculture, but those trends have since been replaced by afforestation (Caspersen et al., 2000; Lepers et al., 2005). In some regions, both forested and agricultural areas are being converted to urban or ex-urban

areas (Brown et al., 2005). The different land uses are likely to have radically different effects on pollinator communities (for examples, see Cane et al., 2006; Chacoff and Aizen, 2006; Frankie et al., 2005; Klein et al., 2002; Kremen et al., 2004; Ricketts, 2004; Winfree et al., 2006), and thus on pollination function (Herrera, 2000; Larsen et al., 2005; Memmott et al., 2004). Grixti and Packer emphasized in their paper (2006) that pollinator assemblages change with successional advances in vegetation, even in urbanized locations. Both community composition and function could be monitored over time along land use gradients.

To calibrate the data obtained from the citizen-scientist program, the professional scientist program would need to involve data collection at a much higher spatial, temporal, and taxonomic resolution in selected areas that overlap with the citizen-scientist program (for example, at urban gardens in the northeastern United States, and on vegetable farms in California—see below). Data for the most part could be specimen-based. Specimens can be identified to species by professional taxonomists in combination with trained para-taxonomists (as in the INBio—Instituto Nacional de Biodiversidad—program in Costa Rica—Janzen, 2004; and the All Taxa Biodiversity Inventory in the Great Smoky Mountains, <http://www.dlia.org/index.shtml>). Such data can be analyzed to determine the degree of association between the citizen-scientist data and the professional scientist data (see also Bhattacharjee, 2005; Danielsen et al., 2005; Gaidet-Drapier et al., 2006).

Citizen-Scientist Programs

A proposed citizen-scientist program could use simple measures of pollinator abundance (such as the number of bees observed at flowers) and pollination function (such as seeds set within fruits or flower-to-fruit ratios on target plants) that could be correctly implemented by nonscientists with minimal training. Inexpensive identification guides could be made available following the online model of “Discover Life” (<http://www.discoverlife.org/>) developed by John Pickering at the University of Georgia, Athens, or Frogwatch (run jointly by the National Wildlife Federation and USGS, <http://www.nwf.org/frogwatchUSA/>).

Programs could be designed and coordinated by scientists, possibly working in public-private partnerships (as is the case with Frogwatch), but implemented by citizens, educators, and students. Such a program could be carried out over a large number of localities, in places that people frequently visit and care about (such as urban gardens and accessible nature reserves). Data can be collected at a relatively coarse temporal and taxonomic resolution, with the goal of long-term annual monitoring of common species and easily recognizable guilds (for example, bumble bees, carpenter bees, and flower flies). Simple, easily implemented observational techniques and

measurements are ideal for this enterprise (for examples, see Methods section below). Use of websites for data entry and to view data is desirable because it allows participants to gain immediate feedback about their work and enhances their motivation (see <http://www.tucsonbirds.org/results/> and <http://www.eman-rese.ca/eman/datamanage.html> for examples). Many excellent examples of existing citizen-scientist monitoring programs provide models (for example, Frogwatch, Monarch Watch, Tucson Bird Count, Illinois Butterfly Monitoring Network, <http://www.bfly.org/>, Canada's Ecological Monitoring and Assessment Network, and others).

Methods

Monitoring Pollinator Status

The professional scientist program could use a combination of specimen-based and observation methods to monitor species abundance (Potts et al., 2005), whereas observational methods are best suited to citizen-scientist programs. Many methods are available for collecting pollinator specimens (Potts et al., 2005), and archiving voucher specimens in a recognized museum collection is a requirement for identification of many species, especially insects. Methods include netting visitors at flowers or trapping pollinators in pan traps, trap nests, or Malaise traps. Netting visitors at flowers is an active sampling method that requires training, and results from this method vary greatly depending on the skill of the netter. All of the other methods are termed passive sampling methods; these do not require great skill and are therefore less subject to inter-investigator biases, but trap placement and collection must be conducted in a highly standardized manner, both within and between sites. Investigators conducting surveys utilize a combination of methods, because a single method is rarely suitable for capturing all species present (Cane et al., 2000; Potts et al., 2005). A standardized protocol developed in North America for sampling bees and other pollinators includes both active and passive sampling methods and is listed at <http://online.sfsu.edu/~beeplot/pdfs/Bee%20Plot%202003.pdf>. For the passive, pan-trap sampling methods, some testing has been conducted to determine the effects of bowl color emission spectrum, bowl size, bowl spacing, type of soap utilized in water, and length of time operated. These tests suggest that yellow, blue, and white UV-emitting bowls are the most effective for trapping pollinators, and that bowls should be spaced at least 5 m from each other for maximum efficiency. Dish-washing detergent should be used in the water to break surface tension. The size of bowl used for sampling duration did not affect the number of pollinators caught (<http://online.sfsu.edu/~beeplot/>). Other standardized protocols involving these and other methods are currently being tested in Europe by the ALARM project (see Box 5-1).

Pollinator communities and populations can also be monitored through visual observation (Potts et al., 2005). Identifying insect pollinators to species on the wing is difficult and requires extensive training in most cases. Thus, monitoring programs relying on visual observation will necessarily be conducted at a coarse taxonomic resolution, except in rare cases involving extremely familiar and exceptionally recognizable species such as *Apis mellifera* or *Danaus plexippus*. Such resolution may be appropriate with a minimum level of training for a citizen-scientist monitoring program for pollinators. Citizen-scientist monitoring programs have also been developed for birds and bats in Mexico and for birds in the United States (for example, Breeding Bird Survey, <http://www.pwrc.usgs.gov/bbs/>).

To standardize sampling, both visual observation and specimen sampling must be conducted only under specified weather conditions (sun, cloud cover, temperature, wind) and time of day or season, in predetermined sampling units of time (for example, a given number of minutes per sample, and samples per site per day) and space (transects or plots) to achieve equal sampling effort between sites (Dafni et al., 2005).

Monitoring Pollination Function

A standard method for monitoring pollination function, well suited to the professional scientist program, is to measure “pollen limitation” (Box 4-2) and in doing so determine whether focal plants become more or less pollen-limited over time or with land-use intensification. Pollen limitation is measured by comparing reproduction on flowers that are experimentally cross-pollinated (by hand-pollinating the flower with pollen from another individual) against control flowers on the same plant and on an adjacent, companion plant that are pollinated under ambient (open) conditions (Dafni et al., 2005; Kearns and Inouye, 1993; Box 4-2). Use of potted plants placed in different environments minimizes differences in plants due to nutrition, genetics, and other variables.

A simpler method that could be used by citizen-scientists is to monitor a self-incompatible, pollinator-dependent plant over time and assess fruit or seed set. Accessible techniques for assessing breeding systems are available in Bernhardt and Edens (2004) and Dafni et al. (2005). Monitoring of pollination function in this manner over time, or along land use gradients, provides a valuable companion data set to that gathered on pollinator abundance trends.

Alternative methods for monitoring pollination function may exist for specific plants and their pollinators. For example, in the deserts of Mexico and the southwestern United States, monitoring of bulbil production by agaves may provide a simple but effective measure of ecosystem pollination services provided by vertebrate organisms, usually bats. Agaves can repro-

TABLE 5-4 Areas for Monitoring Pollination Function Using Agave Bulbil Production

Area	Region or State	Country
Cañon de Santa Elena ^a	Northwestern Chihuahua	Mexico
Central Mexican Highlands ^b	Hidalgo, Puebla, Tlaxcala	Mexico
Chiricahua Mountains ^a	Southeastern Arizona	United States
Chisos Mountains ^a	Big Bend National Park, Texas	United States
Cumbres de Monterrey National Park ^a	Central Nuevo León	Mexico
Hatchet and Animas Mountains ^a	Southwestern New Mexico	United States
Maderas del Carmen ^a	Northwestern Coahuila	Mexico
Sierra Madre Occidental ^a	Northeastern Sonora	Mexico
Sierra Madre Occidental ^a	Northwestern Chihuahua	Mexico
Tehuacán Valley ^c	Southern Puebla	Mexico
Trans-Mexican Volcanic Belt ^b	Morelos, Michoacan, Jalisco, Colima	Mexico

^aArea vegetation dominated by agaves.

^bAgaves locally abundant.

^cAgaves dominate vegetation in the southernmost stretch.

duce vegetatively by producing shoots and rhizomes, or sexually by producing seed-bearing fruits in the stalk after successful pollination (Arizaga and Ezcurra, 1995, 2002), but when pollinators fail to appear, agaves may produce aerial bulbils in the flowering stalk (Arizaga and Ezcurra, 1995). In the Tehuacan Desert of central Mexico, about 5 percent of the plants were never pollinated and instead produced bulbils (Arizaga and Ezcurra, 2002). Monitoring the frequency of bulbil production in selected areas (Table 5-4) may provide a direct indicator of pollinator availability or pollinator service to agaves.

CONCLUSIONS

Current monitoring systems for commercial pollinators, chiefly *Apis mellifera*, exist, but these fail to report or capture all of the necessary data to monitor pollinator status and function. In particular, new questionnaires directed at both the beekeepers and growers need to be developed to capture information on pollination by agricultural commodity. Several monitoring programs also exist for specific taxa or functional groups of pollinators, but many of these programs are either run by individual scientists, and are therefore limited in scale and not sustainable over the long term, or by citizen-scientist groups, and are therefore limited in precision and repeatability.

For pollinators, the ALARM project of the EU provides an excellent model for monitoring and includes development and testing of monitoring methods. In addition, some excellent models exist for a variety of taxa that

couple professional and citizen-scientist collection efforts. The combination of professional and citizen-scientist collection efforts extends the potential for data accumulation, although testing and calibration are needed to assure data quality and validity. A monitoring program could be developed for long-term assessment of pollinator status and function using both professional and citizen-science elements. To address the enormous spatial and temporal variability in pollinator populations as well as the taxonomic impediment, calibration systems could be developed to determine the degree of correspondence between data collected by professional scientists at a fine taxonomic resolution, and data collected by citizen-scientists at a coarser resolution. If valid calibrations can be developed and data quality can be assured, use of both types of data sets is likely to provide more information germane to evaluating pollinator status in time and space at a relatively low cost.

Legacy data (specimens archived in museums) could be captured digitally and utilized (more extensively than has been done to date) to provide a baseline for assessing the status of pollinators in North America today. Areas where substantial legacy data exist should be re-surveyed; areas where contemporary surveys are ongoing should be targeted for digital capture of historical specimen data.

6

Strategies for Maintaining Pollinators and Pollination Services

Although information on the status of most pollinators is incomplete, much can be done to maintain commercial and wild pollinator populations and to prevent future shortages of pollination services. The sustainability of the European or western honey bee (*Apis mellifera*), the principal managed pollinator in North America, could be buttressed through the development and adoption of parasite- and pathogen-resistant stocks of bees. Several developments could help the bee industry reach this goal: use of modern molecular techniques for identifying superior *Apis* stocks, effective methods for the preservation of honey bee germplasm, a suitable infrastructure for maintenance and use of resistant stocks, and adoption of practices by commercial queen producers and beekeepers that are consistent with these goals.

The development of mite- and pathogen-resistant stocks, however, is a long-term solution, one that will require extensive collaboration among researchers, extension personnel, and the queen-and-package industry. In the meantime, beekeepers require immediate relief. Other pest management strategies include programs that mitigate the effects of pesticide resistance in mite populations and cultural and other nonchemical techniques for disease management in commercial hives. Management techniques also must be implemented to reduce the impact of Africanized honey bees, which have begun to colonize areas of the United States critical to the beekeeping industry. The development of methods that support the commercialization of non-*Apis* pollinator species is also a high priority.

For wild, unmanaged pollinators, the most important goals involve conservation and restoration of habitat. Many pollinators can survive in small habitat patches and use the resources in natural areas, wildlands,

and even human-dominated areas including appropriately managed farms, urban parks, and golf courses. Small changes could produce substantial benefits, but basic information on the resource requirements of a wider variety of pollinator species is needed to improve habitat management. Also, economic and policy incentives would encourage the stewards of a wide range of urban and rural areas to adopt pollinator-friendly practices and also to encourage information exchange and outreach. The most effective and sustainable route to stability in pollination services is to identify and implement practices that promote the availability of diverse commercial and wild pollinators.

MAINTAINING COMMERCIAL POLLINATORS

Apis mellifera: Problems and Solutions

The beekeeping industry is at a critical juncture as it faces a suite of challenges that defy easy solution. The parasitic honey bee mite *Varroa destructor*, now ubiquitous in North America, is the single greatest threat to a sustainable supply of healthy and affordable honey bee colonies worldwide (DeJong, 1990; DeJong et al., 1982a, 1984). Major wintertime losses of honey bees in the United States every few years since 1993 (Burgett, 1994; Caron and Hubner, 2001; Finly et al., 1996; Lumkin, 2005) are almost certainly attributable to varroa mite infestation, which was exacerbated by the evolution of resistance to standard miticides. The tracheal mite *Acarapis woodi* also contributes to the periodic catastrophic winter losses, but reliable data on its prevalence in North America are not available. There are effective treatments for management of tracheal mites, including tracheal-mite-resistant stocks of bees (Chapter 3). Problems with tracheal mites, to the extent that they exist, can most likely be ameliorated by improved detection and control among beekeepers.

Another serious challenge to the beekeeping industry is the Africanized honey bee, which has colonized several regions of the United States that are important to the commercial queen-and-package bee industry (northern California and the southeastern United States). The bees also migrate with beekeepers to hospitable wintering grounds. Because the Africanized bees have several traits that are undesirable for beekeeping (Chapter 3), it is imperative that the genotype be prevented from coming to predominance in the United States and Canada. The bees' presence in the southeast—an important area of queen-and-package production for the rest of the United States and a primary wintering ground for beekeepers (Chapter 3)—makes this objective paramount.

Resistant Honey Bee Breeding

A long-term solution to the problems of parasitic mites and honey bee pathogens is the development of resistant stocks of bees. Several traits associated with varroa mite resistance are heritable (that is, available for selection) (Camazine, 1986; Camazine and Morse, 1988; DeJong, 1996; Harbo, 1992, 1993; Harbo and Harris, 1999a,b; Harbo and Hoopingarner, 1995; Harbo et al., 1997; Moritz, 1985; Moritz and Hanel, 1984; Rinderer et al., 2003). Similarly, tracheal mite resistance is a heritable trait (Gary et al., 1990; Page and Gary, 1990). A varroa-resistant stock of honey bees was developed at the U.S. Department of Agriculture (USDA) Agricultural Research Service (ARS) honey bee research laboratory in Baton Rouge, Louisiana (Harbo and Harris, 1999a), and is available commercially as SMR (suppressing mite reproduction) or SMART stock.

Related efforts also have focused on identifying honey bee populations with a long history of exposure to *V. destructor* as a potential source of resistant stock (Rinderer et al., 1999, 2001, 2003). ARS began to import bees from the Primorsky region in far-eastern Russia beginning in the early 1990s (Rinderer et al., 2005). The Russian bees were quarantined on an island off the coast of Louisiana, and they have been subject to further selection. The Russian bees exhibit a high degree of varroa mite resistance (Rinderer et al., 2003, and references therein), and they are now available commercially.

Resistance to American foulbrood and other bee pathogens was shown to be heritable in the 1930s (Park, 1936). Although other traits contribute to foulbrood resistance (Spivak and Gilliam, 1998a,b), the principal mechanism is hygienic behavior (Rothenbuhler, 1964). Stocks that exhibit hygienic behavior have been developed at least three times since the 1930s (Park et al., 1937, 1939; Rothenbuhler, 1964; Spivak and Reuter, 2001). Hygienic behavior also could operate in mite resistance (Boecking et al., 2000; Harbo and Harris, 2005; Spivak and Reuter, 2001), and the University of Minnesota has developed hygienic stocks that are available commercially.

Another challenge to the bee industry is the synthesis of results from federal and academic research into sustainable commercial queen-and-package operations. There are well-developed methods for quantifying resistance to mites and pathogens (Harbo and Harris, 1999a; Harbo et al., 1997; Spivak and Downey, 1998; Spivak and Gilliam, 1998a,b) and for breeding and maintaining resistant stocks (Harris et al., 2002; Page and Laidlaw, 1982a,b; Page et al., 1983, 1985). Perusal of trade journals reveals beekeepers' interest in mite-resistant stocks of bees and the low availability of such stock: Several suppliers advertise Russian, SMR, or hygienic bee stocks, but there are no data on the number or quality of queens available. It is not clear why resistant stocks have not yet been widely adopted (Sheppard, 2006), but it is possible that the impediments include the difficulty of maintaining inbred

lines, the negative consequences of selecting one trait over others that are commercially important (Page and Laidlaw, 1992), and the time and effort involved in replacing queens (Laidlaw, 1992).

Of particular importance is the lack of locally adapted stocks. Typically, although not universally, southern queen producers use stocks that perform well in the warmer south but that might not do well in the north, where winters are more severe. This is especially problematic for stocks that are affected by tracheal mites or diseases such as chalkbrood, both of which affect bees more in the cooler, damper regions of the north (Flores et al., 1996). Establishing locally adapted populations of bees is difficult because more than 500,000 queens are shipped each year throughout the country from southern production sites (Schiff and Sheppard, 1995, 1996).

Instrumental insemination (Laidlaw, 1992) is ideal for bee-breeding programs (development and maintenance), although it is more costly than is natural mating. Moreover, the honey bee mating behavior presents a challenge to the development and maintenance of selected lines of honey bees. Honey bee queens are naturally polyandrous (Winston 1987), mating with 7–17 drones on 1–5 mating flights, usually within the second week of life. Queens and drones fly to discrete spaces in drone congregation areas, located some distance above the ground and away from their nests. Mating takes place as the queen flies through one or more drone congregation areas, where the sources of drones are uncontrolled. It is not clear whether some percentage of mating with a specific desired stock is necessary to ensure a mite- or pathogen-resistant colony (Box 6-1) and likely depends on the genetic mechanisms involved (dominance, additive, epistasis).

Most commercial queen producers probably do not use resistant stocks, and most queens shipped throughout the United States apparently still come from susceptible stocks of bees. Susceptible queens also produce drones that flood local mating areas, so it is difficult to establish a sustainable resistant population.

Genetic Solutions to Problems with Mites and Pathogens

Genomics and germplasm preservation could be used to facilitate the development and maintenance of selected honey bee stocks. The traditional breeding process could be augmented through the use of genetic markers (expressed sequence tags and quantitative trait loci) for desirable traits. Markers already have been identified for defensive behavior (Hunt et al., 1998) and for hygienic behavior (Lapidge et al., 2002), and more research could facilitate development of commercially viable selected stocks of honey bees. The recent sequencing of the honey bee genome by the Baylor College of Medicine (The Honeybee Genome Sequencing Consortium, 2006) and

BOX 6-1

**Development and Maintenance of Selected Stocks:
Controlled Mating**

The development and maintenance of selected stocks and breeder queens require controlled mating, generally through instrumental insemination (Laidlaw, 1992). Breeder queens (selected queens inseminated with semen from selected drones) are transferred or sold to commercial queen producers who use them to produce large numbers of production queens for sale to beekeepers. The parentage of the production queens is controlled through the use of breeder queens. Before a production queen is sold to a beekeeper, it is first mated to several drones, and the mating of production queens is invariably natural. Because commercial queen producers cannot completely control the sources of the drones that mate with their production queens (Laidlaw and Page, 1998), the queens often mate with drones from unselected stocks of local wild bees or from colonies belonging to other beekeepers. Thus, production queens will often produce hybrid workers that do not exhibit the desired traits or that do not exhibit those traits to the desired extent, depending on the genetic basis of the variation under selection (for example, dominance, additive, epistasis).

The percentage of matings that must occur with a specific desired stock to ensure a mite or pathogen resistance in a colony is not known and could depend on the trait. Some work suggests that open-mated queens from selected stocks can produce colonies with useful—but incomplete—mite resistance (Harbo and Harris, 2001; see also Spivak and Reuter, 1998, and Spivak et al., 1995, for response to American foulbrood), but another report suggests that both male and female parents should be from selected stocks (Harris and Rinderer, 2004).

Although instrumental insemination is currently complicated for use in commercial queen production, there are other options for controlling commercial mating—drone saturation and isolation (Laidlaw and Page, 1998). The former achieves varying degrees of controlled natural mating by stocking mating areas with large numbers of drone source colonies from the desired selected source (Hellmich, 1986, 1991; Hellmich et al., 1988). The latter uses isolated mating yards to control mating. The opportunity to employ isolation is limited because a separation of several kilometers from other sources of drones is required.

related developments in honey bee genomics (Robinson et al., 2005) provide outstanding resources for these efforts.

Maintaining selected stocks of honey bees is difficult because of the generally uncontrolled mating behavior of queens and because queens have relatively short and unpredictable lives of 1–3 years (Seeley, 1985). Given the ephemeral nature of honey bee stocks, honey bee germplasm (sperm, eggs, embryos) is an ideal candidate for preservation, which would allow stakeholders an economical way to maintain large quantities of desirable germplasm from a nearly unlimited number of sources. The benefit seen in the increased access to resources would well justify the investment required to identify or develop the germplasm. This work would fit within the mission of the USDA National Animal Germplasm Program (<http://www.ars-grin.gov/animal/>), which coordinates and supports the cryopreservation of U.S. animal genetic resources (Blackburn, 2002). Preservation of honey bee germplasm has been attempted, so far with limited success (Collins, 2000, 2004).

Transition to Resistant Stocks

Converting the current U.S. honey bee population to one that is resistant to parasites and pathogens is an enormous challenge that would require unprecedented cooperation among queen producers and consumers, federal and university research facilities and extension programs, and, most important, beekeepers. A successful transition would require improved identification methods, including the use of genetic markers in mass screening for desirable traits; new stocks that are viable in several regions; an industry infrastructure that maintains superior stocks; and a mechanism for third-party certification of new product lines. Certification of breeder stock, mating technology, production methods and facilities, and commercially produced bees and queens would be necessary.

Managing Miticide Resistance

Pesticide resistance has become the major problem for the management of parasitic mites. Populations of *V. destructor* that exhibit resistance to fluvalinate (Baxter et al., 1998; Elzen et al., 1998, 1999a,b,c,d; Hillesheim et al., 1996; Macedo et al., 2002), coumaphos (Elzen and Westervelt, 2002; Milani and Della Vedova, 1996; Pettis et al., 2004), or amitraz (Elzen et al., 1999c, 2000) are widespread.

Resistance management programs would provide beekeepers with a significant tool for mite management. Such programs could be built around results from several areas of research, including projects on the mechanisms and management of resistance to various pesticides (Gerson et al. 1991; Ting et al. 2003; Wang et al. 2002; Wu et al. 2003), the identification of genetic

correlations among resistance mechanisms, determination of the fitness consequences of pesticide resistance, and determination of optimal intervals for pesticide rotation (Hall et al. 2004).

The industry also could benefit from the development of synergists to inhibit enzyme-based resistance in mite populations, thereby restoring the effectiveness of existing miticides. And the identification of new, less toxic pesticide compounds derived from natural products would provide beekeepers with still more options. In particular, the work should focus on improving the efficiency and reliability of such commercial products as Mite-Away II and other soft chemicals (Apiguard and Api-Life VAR).

The design of resistance management programs could follow up results from research projects outlined above. Although there are no comprehensive programs for beekeepers, there is considerable literature that could be used as a starting point for research on pests of bees (see Batabyal and Nijkamp, 2005; Benting et al., 2004; Comins, 1986; Elzen et al., 1999b; Georghiou, 1980; Green et al., 1990; Hall et al., 2004; MacDonald et al., 2003; Phillips et al., 1989; Thompson, 2003; Walker-Simmons, 2003; Williamson et al., 2003).

The tracheal mite has dropped into relative obscurity over the past decade, overshadowed by problems with varroa mites. The current effects of tracheal mites on honey bee populations are not known. Fortunately, several remedies are available for control of tracheal mites, including “grease patties” (made from vegetable shortening and granulated or powdered sugar) (Baxter et al., 2000; Calderone and Shimanuki, 1995; Liu and Nasr, 1993; Wilson et al., 1989), formic acid (Baxter et al., 2000; Feldlaufer et al., 1997; Hoppe et al., 1989), and menthol (Baxter et al., 2000; Duff and Furgala, 1993; Wilson et al., 1989, 1990). Amitraz, although not currently marketed, also can be effective against tracheal mites under some circumstances (Duff and Furgala, 1993; Wilson and Collins, 1993). Treatment results have been mixed (Duff and Furgala, 1993; Scott-Dupree and Otis, 1992), and honey bee populations have evolved resistance to tracheal mites (Gary et al., 1990; Page and Gary, 1990), an attribute that likely has contributed to a reduction in concern about this pest.

There is an additional economic benefit to deploying mite-resistant bees and reducing pesticide use—over and above the savings realized from eliminating the need to purchase chemical pesticides. The use of resistant stocks allows beekeepers to eliminate pesticide use, and some beekeepers could potentially sell their products at a premium (NRC, 2000).

Other Methods of Managing Parasites and Pathogens

Nonchemical control methods—such as cultural methods or biological control—offer many advantages for beekeepers. Combined with third-party

certification of honey (as pesticide-free or organic, for instance), those methods expand the beekeepers' options in the marketplace, enabling them to take advantage of the more lucrative trade in natural foods. Among the cultural methods for mite control, drone brood removal, which exploits mite preference for drone brood, can be effective albeit labor-intensive (Calderone, 2005). The Beltsville screen insert, a piece of wire mesh inserted 3–5 cm between a hive's bottom and its bottom board, traps the mites that typically fall to the bottom of the hive as bees groom to rid themselves of mites. The insert prevents the mites from climbing back up to reinfest the bees. The screen insert has yielded mixed and generally disappointing results (Ellis et al., 2001; Harbo and Harris, 2004; Pettis and Shimanuki, 1999; Rinderer et al., 2003), but it could become an effective management tool if it were combined with pesticides that have a rapid knockdown effect for application during honey-producing months.

The fungal pathogens *Hirsutiella thompsonii* and *Metarhizium anisopliae* have shown promise as potential biological control agents for varroa mites (Kanga et al., 2003a,b), but problems with the pathogens' sensitivity to temperature and spore distribution within hives remain unsolved. If these could be overcome, biological control could become a viable option for managing parasitic mites.

Perhaps even more important than developing new treatments for bee diseases and parasites is reinforcement of regulations aimed at prevention. Protection of North America against invasive pests and diseases from abroad is the cornerstone of pollinator protection on the continent, but existing regulations should be strictly enforced and strengthened to remain effective. The Federal Honey Bee Act of 1922 "prohibits the entry of honey bees from countries where diseases and parasites harmful to honey bees are known to exist" (USDA-APHIS, 2002). The act authorizes the Animal and Plant Health Inspection Service (APHIS) to regulate importation of honey bees in the United States. In 2004, APHIS changed the regulation to allow honey bee packages from Australia and New Zealand to be imported to pollinate California almond groves (USDA-APHIS, 2004).

Although honey bee colonies from Australia and New Zealand can offer a short-term benefit in the pollination marketplace, great care must be exercised to ensure that they do not carry new pests, parasites, pathogens, and predators. APHIS and corresponding agencies in Canada and Mexico should conduct periodic, coordinated monitoring of honey bee populations to determine whether specific pests are present. Target species for monitoring should include *Tropilaelaps clareae* (parasitic mite), *Hyplostoma fuliginosus* (large hive beetle), *Varroa* spp. and *V. destructor* haplotypes that are not present in North America, *Apis mellifera scutellata* (African honey bee), *Apis mellifera capensis* (another potentially invasive subspecies of honey bee from South Africa), and other *Apis* species. APHIS could coordinate the

efforts with cognate agencies in Mexico and Canada. State departments of agriculture should be included in the development of monitoring programs and could provide valuable personnel. Shipments of bees from countries or territories that have pests that are not already present throughout North America should not be permitted if long-term safeguarding of North American pollination capacity is a priority.

APHIS should carefully assess the integrity of inspection in countries interested in supplying bees to North America, and it should collect and analyze samples of adult and immature honey bees from producers who wish to ship to North America. Sampling in the countries of origin is necessary because the bees could have pests that are currently unidentified and therefore not on the list of target species. Also, North American countries should proceed with research on honey bee pests in the potential source countries that have not yet arrived in North America to prepare the countries' beekeeping industries for possible or eventual introductions.

Africanized Honey Bees

The consequences of the Africanized honey bee (AHB) infiltration of U.S. and Canadian honey bee populations are difficult to predict. However, uncertainty and precedent in other nations suggest that it is prudent to prepare for the worst. There are three general methods for managing AHBs: eradication, genetic isolation, and breeding (<http://www.ces.ncsu.edu/depts/ent/notes/Bees/ahbactionplan2001.pdf>). Several states, including North Carolina, have developed action plans that include recommendations for best management practices for beekeepers, and procedures for abatement, quarantine, outreach, and first-responder training. Other states should develop similar plans, and much of the information they need is available from existing resources.

Eradication is most effective against confirmed or suspected founder colonies that are inadvertently imported by truck or ship, but before the Africanized bees can become established. Genetic isolation is achieved through various controlled-mating techniques—such as geographic isolation, instrumental insemination, and drone saturation (Laidlaw and Page, 1998). Geographic isolation requires European honey bee production apiaries to be established at a distance from AHB colonies that is sufficient to prevent mating of the European queens with the Africanized drones. Queen-and-package producers might be able to use this method to a limited degree by placing operations in places that are so far free of Africanized bees: the northern United States, Hawaii, Canada, Australia, and New Zealand. Northern U.S. and Canadian operations could be of limited use, however, because the colder weather prevents production of queens and packages until late in the season. The United States began to import honey

bee packages from Australia and New Zealand for early-season pollination after winter losses in 2004–2005 (Sumner and Boriss, 2006). Australia, New Zealand, and Hawaii could be important sources of uncontaminated germplasm in the future, but extreme vigilance would be needed to ensure that additional invasive diseases or pests not be introduced.

A second way to control mating is through instrumental insemination (Laidlaw, 1977), which allows for control of male and female sources of germplasm and for maintenance of a secure, closed breeding population. Instrumental insemination is a highly effective tool in the hands of qualified practitioners and it is effective for the maintenance of domestic supplies of germplasm that is free of AHB traits. However, it is impractical for the production of commercial queens for sale to beekeepers: it is too time-consuming and labor-intensive to be profitable (Laidlaw and Page, 1998).

The final method for controlling mating is drone saturation: flooding an area with enough drones from a desired source to enhance the probability that young queens will mate with them. More research is required, however, to determine the degree of mating control required to produce behaviorally acceptable colonies (Guzmán-Novoa and Page, 1994a).

Beekeepers are aware of liability issues that could result from stinging incidents that involve Africanized bees. Guzmán-Novoa and Page (1994b, 1999) have reported that selective breeding within Africanized populations can result in a reduction in defensive behavior. However, continuous breeding selection could be necessary to suppress defensive behavior, especially where AHB stocks are prevalent.

Integrated Pest Management

Integrated pest management (IPM; Kogan, 1998) provides a unifying framework for the management of many agricultural pests, including those of honey bees. IPM coordinates the use of several pest control methods for sustainable, economically feasible management. Whenever possible, IPM uses reliable pest-sampling methods and economic injury thresholds to guide treatment decisions. IPM is desirable because it allows beekeepers to use pest information to avoid economically unnecessary applications of pesticides and antibiotics, thereby extending the long-term utility of those products by reducing the rate at which resistance evolves. It also allows beekeepers to reduce or eliminate pesticide residues in hive products.

Each sector of the beekeeping industry will require an IPM program to fit its size (the number of colonies) and its marketing goals (commercial or natural foods). American foulbrood is one disease that is effectively treated with IPM approaches. The combination of cultural methods with inspection programs and the proper use of antibiotics provides good results for control (Goodwin and Van Eaton, 1999). Continued extension efforts should be en-

couraged to widen acceptance of IPM of parasitic mites, especially by large commercial operators. The future of IPM's application in the industry will depend on the development of additional treatments and on the creation of economic incentives to compensate for the additional costs involved.

Extension activities provide a primary mechanism for informing beekeepers about pest management options and the best ways to implement them. Extension apiculturists should encourage the use of IPM whenever possible, and extension personnel should encourage beekeepers to demand third-party certification of resistant stock from commercial queen producers. Extension efforts directed toward queen breeders and commercial queen producers should emphasize methods for stock development and maintenance and the use of controlled mating, primarily through geographic isolation and drone saturation.

ARS Honey Bee Research

Much of the applied research on honey bees in the United States is conducted in ARS honey bee laboratories. Research funding has increased from \$5.6 million in 1996 to \$9.2 million in 2006, although the number of full-time scientists has declined since 2003 (Table 6-1). Some of the approaches to preventing or reversing pollinator decline outlined in this chapter depend on strong ARS involvement in honey bee research. Maintaining current research support and restoring lost scientist positions—with a special focus on honey bee pollination—at ARS is critical to pollinator conservation and restoration.

TABLE 6-1 Funding and Staffing ARS Bee Research

Fiscal Year	Funding (\$ U.S.)	Full-Time Permanent Staff Scientists
1996	5,574,000	23
1997	5,913,000	23
1998	6,380,000	23
1999	6,599,000	26
2000	7,009,000	26
2001	7,629,000	27
2002	8,037,000	25
2003	8,450,000	28
2004	8,844,000	27
2005	8,861,000	27
2006	9,227,000	24

SOURCE: USDA-ARS.

Government Intervention

Although beekeepers have faced recent substantial increases in the cost of mite control and hive transportation (Chapter 3, Chapter 4), those expenses have been offset somewhat by higher pollinator rental rates and, in some years, by higher honey prices. The higher prices signal shorter supplies of honey bees. Honey bee populations recovered after the winter kills of 1995–1996 and 2001–2002 (USDA-NASS, 1999, 2004a) and pollinator rental rates have increased as have competitive honey prices. Continuing indirect federal price supports through the loan deficiency payment and marketing assistance loan programs (USDA-FSA, 2006) also strengthen the market. Beekeepers can be expected to re-establish the honey bee colonies lost during the 2005–2006 winter. In general, although honey bee colony numbers are much more volatile from year to year since the arrival of the varroa mite (Chapter 2), the market for honey bee pollination services appears appropriate, and that signals help in stabilizing the number of pollinator colonies available (Sumner and Boriss, 2006). However, government intervention could reduce volatility by encouraging research, extension, and certification efforts; by creating stricter controls for importation of honey bees from other countries; and by better monitoring of honey bee colonies and pollination services (Chapter 5).

Faced with managing the varroa mite threat to the North American honey bee population, the beekeeping industry might find that its funds alone are insufficient to cover immediate research needs. Special, limited-term federal support should be made available through a competitive research program targeted at honey bee genetics and management to protect populations. The program could be administered by the USDA National Research Initiative Competitive Grants Program or by the National Science Foundation. Given the targeted agricultural nature of the problem, however, a USDA program would be more suitable. Long-term, programmatic research support should continue through ARS.

The effects of increased research for improved varroa mite management will be emasculated in the absence of effective communication with the honey bee industry. The recent reductions in federal funding for state extension programs leave two avenues for improving communication. First, state land grant universities should seek ways to cooperatively finance positions for honey bee extension specialists, who could then increase the benefits of research through education and outreach. Second, the honey bee industry, represented by the American Beekeepers Federation and the American Honey Producers Association, should continue and intensify its efforts to communicate advances in honey bee hygiene and management information. The industry also could collaborate with researchers to help

identify obstacles to the transition to IPM-based beekeeping, with resistant stock as a foundation.

Continuous protection against invasive pests and diseases from abroad is crucial to pollinator protection on the continent. The federal Honeybee Act of 1922 authorizes APHIS to regulate imports. The 2004 revision (USDA-APHIS, 2004), prompted, in part, by honey bee shortages in California almond groves, led to extensive APHIS collaboration with the Australian Quarantine and Inspection Service and New Zealand's Ministry of Agriculture and Forestry to establish rigorous inspection and quarantine procedures (USDA-APHIS, 2004). Rigorous enforcement of sanitary rules on honey bee colony and queen importation must continue, along with protection against interstate transmission of pests. The revision (USDA-APHIS, 2004) permits importation of other pollinator bee species (*Bombus impatiens*, *B. occidentalis*, *Megachile rotundata*, *Osmia lignaria*, and *O. cornifrons*). Importation of these bees is regulated to prevent the introduction of new of diseases, parasites, and pest species.

Industry Initiatives

Beekeepers and the crop producers who require pollination have a special interest in the health of honey bees. The main fundraising mechanism available to U.S. agricultural producers for research and promotion is the Commodity, Promotion, Research and Information Act of 1996, which authorizes "check-off" programs administered by the USDA Agricultural Marketing Service (AMS) but managed by an industry board (USDA-AMS, 2005). Since its creation in 1987 through a USDA-administered referendum of honey producers, the National Honey Board has administered a check-off program that pools revenues from the fee of a penny per pound of honey that is collected from producers who sell at least 3 tons of honey in a year. The Honey Research, Promotion, and Consumer Information Order collects the funds for marketing and research to reduce production costs and to enhance demand for honey (USDA-AMS, 2004). The specific focuses are honey research and promotion, not work on pollination or pollinators.

Given the increasing importance to beekeepers of revenues from pollination fees and the importance of honey bee pollination to producers of almonds and many other fruit and vegetable crops, the two groups might consider joint fundraising to focus support on pollination-related research and education. Research on methods to mitigate damage caused by parasitic mites and to ensure strong colonies each spring are among the relevant topics that joint support could fund. Another is research on honey bee stock development and maintenance.

Non-*Apis* Commercially Managed Bees

The potential for using wild bees as managed crop pollinators has long been known (Bohart, 1972a) and several approaches have been explored (Bosch and Kemp, 2002; Macfarlane et al., 1994; Stephen, 2003; Torchio, 2003). There is an extensive body of published work on methods of rearing wild bees (Griffin, 1993; Hughes, 1996; Maeta and Kitamura, 1981; Strickler and Cane, 2003; van Heemert et al., 1990) that provides a strong foundation for efforts to identify and cultivate commercial pollinators among the large number of wild bee species (Strickler and Cane, 2003).

Several native and nonnative species currently are being used commercially or have potential for use as agricultural pollinators in North America (Chapter 1). Among the native North American bees, *Osmia lignaria* is an efficient and cost-effective pollinator of sweet cherry, plum, and prune (Bosch and Kemp, 1999) that has demonstrated potential as an almond pollinator (Bosch et al., 2000; Torchio, 1981a,b, 1982). *O. ribifloris* is an effective pollinator of blueberry (Sampson and Cane, 2000; Sampson et al., 2004; Stubbs et al., 1994; Torchio, 1990). *O. aglaia* can be an effective pollinator of cultivated blackberry and raspberry (Cane, 2005), and *O. excavata* and *O. jacoti* have potential as commercial pollinators (Wei et al., 2002). Bumble bees and *Andrena* spp. are better pollinators of lowbush blueberry than are honey bees (Javorek et al., 2002). Bumble bees are also highly efficient greenhouse crop pollinators (Box 3-1; Free, 1993).

O. cornifrons, the hornfaced bee, is an Asian species used extensively for apple pollination in Japan (Batra, 1982; Maeta, 1990; Sekita, 2001) that has good potential for North American pear pollination (Maeta et al., 1993). It was imported into the United States in 1977 (Batra, 1979), but it has not become established as a commercial pollinator. The alfalfa leafcutter bee, *Megachile rotundata*, introduced from Eurasia, is superior to honey bees for alfalfa pollination (Cane, 2002; Tepedino, 1997). *M. rotundata* also can be an effective pollinator of blueberry (MacKenzie, 1997; Stubbs and Drummond, 1997a) and oilseed rape (Soroka et al., 2001) but not cranberry (MacKenzie, 1997).

Although USDA no longer introduces exotic bees to North America for development as commercial pollinators, prospecting among native fauna for new agricultural pollinators is an important way to encourage redundancy that will promote pollination services and food security and stability. Although prospecting programs have been in operation for 50 years at ARS and several university laboratories, the search for, biological evaluation of, and development of propagation and rearing methods for alternative bee pollinators have resulted in the wide-scale propagation of only a single species. The alfalfa leafcutter bee was propagated successfully as the result of development of trap nest technology at the ARS Bee Biology and Systematics

Laboratory in Logan, Utah (Bohart, 1962, 1972 a,b; Bohart and Pedersen, 1963). The entire contemporary U.S. alfalfa leafcutter bee industry results largely from this pioneering work by a few USDA and Canadian agricultural scientists who, because of its behavior in Eurasia, recognized the leafcutter bee as a legume crop pollinator. Strickler and Cane (2003) discussed lessons learned from past experience on developing alternative pollinators and offered suggestions to guide future effort.

In view of the effort required to develop new commercially managed pollinators, to complement efforts at the Logan laboratory, ARS could well benefit from creating positions in research entomology for the ARS fruit and vegetable laboratories across the United States. Their work might identify candidate pollinators for the major crops requiring pollinators in different regions, study the life history of promising species, identify potential pest problems, and develop viable management and rearing methods for commercial use of those species.

In addition to increasing the effort to identify new commercial pollinators, research investments are needed to prevent declines in existing commercially important species. The alfalfa leafcutter bee was devastated by chalkbrood—a fungal disease—and the absence of any successful management strategy (Chapter 3) should spur research to develop tools for an effective response.

U.S. bombiculture, the rearing of bumble bees, faces many more serious problems than does megachileculture—the rearing of leafcutter bees. Bumble bees are susceptible to some of the same diseases and parasites that plague honey bees, and disease limits their utility as commercial pollinators. Infections of the bees can complicate long-term maintenance of captive colonies. Two native species (*B. occidentalis* and *B. vosnesenskii*) have been evaluated, mass reared, and used as pollinators in the United States, but infections of *Nosema* and other pathogens in commercial insectaries led to discontinuation of these efforts (Thorp, 2003; Winter et al., 2006). Today, the only bumble bee raised for commercial greenhouse tomato pollination in the United States is *B. impatiens*, which is native to the eastern United States. Multinational agribusinesses have developed large-scale insectaries for year-round production of bumble bee colonies in Europe, Israel, Canada, Mexico, and the United States (primarily *B. terrestris* in Europe, *B. impatiens* in the eastern United States). In 2005, about 90,000 hives—from all suppliers of bumble bees—supplied bumble bees for pollination throughout Mexico, the United States, and Canada (René Ruiter, Koppert Biological Systems, personal communication, February 2006). U.S. bombiculture presents risks to native bees that could be greater than the risks posed by U.S. apiculture to honey bees (because there are no native North American *Apis* species). If managed nonnative bumble bees escape, hybridization and competition with native *Bombus* species could occur (Thorp, 2003; Winter

et al., 2006). The potential for such hybridization between European and Japanese species has been demonstrated in the laboratory (http://www003.upp.so-net.ne.jp/consecol/english/goka_report/goka_report.html).

Large-scale transportation of native and exotic bumble bee colonies among regions of North America and internationally is already thought to be a source of introduced pathogens in native North American *Bombus* species (Chapter 3; Thorp, 2003). During the initial stages of bombiculture development in the United States, native bumble bee queens of *B. occidentalis* captured in the United States were transported to Holland and used to start colonies that were later returned to the United States (René Ruiter, Koppert Biological Systems, personal communication, February 2006). The concern has been raised that the bees' reintroduction carried new parasites or diseases (Chapter 3) into the United States. According to Colla and colleagues (2006), there is evidence that "commercially-reared bumble bees have higher prevalence of various pathogens than their wild counterparts. Several studies have found that the intestinal protozoa *Crithidia bombi* Lipa and Triggiani (Kinetoplastida: Trypanosomatidae) and *Nosema bombi* Fantham and Porter (Microsporidia: Nosematidae), and the tracheal mite *Locustacarus buchneri* Stammer (Acari: Podapolipidae) are far more abundant in commercial than wild bumble bees." Because bumble bees often escape from and forage outside greenhouses where their colonies are used for tomato pollination, they could transmit diseases to wild colonies of the same and other *Bombus* species. Colla and colleagues (2006) reported a significantly higher incidence of infection with parasites and pathogens in various bumble bee species collected near greenhouses, than in individuals collected farther away. In Japan, Niwa and colleagues (2004) documented the transfer of pathogens from European to Japanese bumble bees, and comparable "pathogen spillover" might have caused or contributed to the recent decline and extirpation of several bumble bee species in the subgenus *Bombus* and to the likely extinction of *B. franklini* (Chapter 3; Colla et al., 2006; Thorp, 2005; Thorp and Shepherd, 2005).

Recently, bumble bee rearing in the United States has been accomplished without international bees in facilities certified monthly by APHIS to be free of known bee diseases (René Ruiter, Koppert Biological Systems, personal communication, February 2006). The United States and Canada also have blocked imports of nonnative bumble bees (such as *B. terrestris*). Industry groups are lobbying the Mexican government to allow introductions of *B. terrestris* (from Europe) into Mexico for tomato pollination in greenhouses (Winter et al., 2006). Restriction of bumble bee transfers both within the United States and from other countries is advisable because of the potential for disease transmission to managed and native wild bumble bee species and the invasiveness of some species (such as *B. terrestris*; Dafni and Schmida, 1996; Hingston and McQuillan, 1997, 1998).

MAINTAINING WILD POLLINATORS

Wild pollinators are mobile organisms that often use many resources in noncontiguous habitats. Some butterflies visit suburban gardens for nectar but oviposit on the foliage of tree species in forest habitats. Many species of hummingbirds that breed in the United States and Canada overwinter in Mexico (Nabhan et al., 2004; Shepherd et al., 2003). Maintaining diverse communities of wild pollinators therefore requires an understanding of various habitat needs and of managing habitats and landscapes to provide necessary resources (Table 6-2). Populations of pollinators can be supported if habitats are managed to provide food, and areas for nesting, overwintering, and breeding (Dover, 1991; Erickson and West, 2003; Evelyn et al., 2004; Fenton, 1997; Schultz and Dlugosch, 1999; Scott, 1986). Because pollinators are mobile, the area over which they forage, disperse, and migrate must be considered in strategies to maintain populations. Adequate resources must be available within foraging and dispersal areas (Westrich, 1996) and along migratory routes (Nabhan et al., 2004).

Managing pollinator populations and communities requires planning and action locally, regionally, and across continents. Because of their ecological and economic significance and because they are in some respects better known than are many other wild pollinators, bees can serve as a paradigm group to illustrate how multiscale approaches can be implemented in habitat restoration, conservation, and management.

Resource Requirements for Bee Species

All native and introduced bee species, whether solitary or social, require the correct balance of water, floral hosts that offer sufficient pollen and nectar of the correct types (Roulston and Cane, 2000; Roulston et al., 2000), nest-building materials (leaves, resins, sap, gums, floral oils, essential oils, bark, plant trichomes, old mouse nests, snail shells, mud, sand, pebbles), and nesting substrates (O'Toole and Raw, 1991; Roubik, 1989; Shepherd et al., 2003) to survive as adults and rear their larval broods (Michener, 2000).

Michener (2000) provided a comprehensive review of floral resource requirements for bees. Bees obtain pollen and nectar from cultivated and wild plants. Pollen (usually moistened with nectar or floral oil) is used to feed larval bees, and nectar is used to fuel the flight of adults. Many solitary bees are active above ground as adults for only a few weeks or months. Oligolectic bees specialize on one or a few closely related species within a genus of flowering plants; polylectic bees collect pollen from an array of unrelated plants. Species with long flight seasons are usually polylectic and include the long-lived carpenter bees and euglossine orchid bees, those that produce multiple generations within a season, and highly social bees with annual or permanent colonies (honey bees, bumble bees, stingless bees).

TABLE 6-2 Pollinators and Resource Requirements

Pollinator Group	Resource Function	Resource
Honey bees, bumble bees, bats ^a	Nesting, roosting sites or substrates	Cavities (underground, hollow trees), large caves, mines
Hummingbirds ^b	Nesting, roosting sites	Trees (horizontal branches with shelter from night sky)
Nonsocial bees, wasps ^c	Nesting sites or substrates	Bare ground, vertical cliffs or ditch banks, adobe walls
Large and small carpenter bees, leafcutter bees, mason bees ^d	Nesting sites or substrates	Soft woods, pithy twigs, beetle burrows
Bumble bees ^{a,e}	Nesting sites	Rodent, mouse nests
Flies	Adult food	Pollen, nectar
Flies	Larval food	Insects, organic matter, water
Leafcutter and mason bees (European) ^f	Nesting sites	Plant galls, snail shells
Nonsocial bees, wasps	Nesting sites	Sand dunes, sand or burrow pits, gravel pits, quarries
Highly eusocial bees, honey bees, bumble bees, stingless bees	Building materials	Glandular secretions (beeswax, exocrine secretions, Dufour's)
Nonsocial bees, some wasps; mason bees, leafcutter bees, masarid wasps, potter wasps	Building materials	Mud, clay, sand
Leafcutter bees, mason bees, masarid wasps	Building materials	Debris (bark, floral parts, seeds, dead insect parts)
Nonsocial bees, some wasps	Building materials	Water (mixed with soil to make mud)
Leafcutter bees, mason bees	Building materials	Leaves cut into pieces or masticated
Leafcutter bees, especially anthidiines (carder bees)	Building	Plant hairs (trichomes)
Leafcutter bees, <i>Apis</i> , <i>Melipona</i> , <i>Trigona</i> , orchid bees	Building materials	Floral, plant resins
Orchid bees	Pheromones	Essential oils, such as monoterpenoids collected by males
Bees	Food, building materials	Floral oils (<i>Clusia</i> , <i>Dalechampia</i> , <i>Krameria</i> , Malpighiaceae)
Birds, some bats, bees, masarid wasps, butterflies, flies	Food	Pollen, nectar
<i>Centris</i> , <i>Epicharis</i> , <i>Paratetrapedia</i> bees	Food, building materials	Floral oils (<i>Clusia</i> , <i>Dalechampia</i> , <i>Krameria</i> to mix with pollen)
Wasps, Pompilidae (spider wasps)	Larval food	Paralyzed spiders
Parasitic, nonparasitic wasps	Larval food	Insect prey
Butterflies, moths	Larval food	Leaves, other plant parts (often taxonomically restricted)
Ants	Adult, larval food	Nectar, honeydew, insect prey
Beetles	Adult, larval food	Pollen, nectar, food bodies, organic matter

TABLE 6-2 Continued

Pollinator Group	Resource Function	Resource
Thrips	Adult, immature food	Floral tissue, leaves, pollen, nectar
Hummingbirds	Food	Nectar, small insects
Hummingbirds	Building materials	Spider webs (silk), lichens, fibers

^aMichener, 1974.

^bEhrlich et al., 1988.

^cMichener, 2000.

^dKrombein, 1967.

^eHeinrich, 2004.

^fO'Toole and Raw, 1991.

The bee species might require floral resources for weeks or months, so a diversity of floral sources must be available; at least some of the flowering plants should have overlapping blooming periods that encompass the bees' long flight periods. For social bees that overwinter as adults (bumble bees, honey bees), the temperate bloom of fall-blooming asteraceous species (goldenrods) are nectar and pollen sources that provide protein and carbohydrate resources essential for winter survival (Shepherd et al., 2003; Vaughan et al., 2004).

Bee species vary in floral resource requirements, and there is a wide variation in nesting habits. Many dig nests in the ground (Halictidae, Andrenidae), others occupy abandoned rodent nests (*Bombus* spp.), some use preexisting tunnels or cavities in dead tree trunks and limbs (Megachilidae, some Apinae), and others actively excavate cavities in wood (Xylocopinae). The diversity of a bee community is tied to the availability of different nesting substrates (Potts et al., 2005).

Most North American bees are ground-nesting. Like their more familiar sand wasp relative, they vary by species in nest site selection criteria (Cane, 1991; Michener, 2000; O'Toole and Raw, 1991). Some ground-nesting bees prefer to nest in open, horizontal areas of soil devoid of vegetation or debris; others seek small areas of bare soil within lawns or nest in vertical banks, either naturally occurring ones or those formed by adobe structures, wood frame houses, and other buildings. Patches of bare earth warmed by the sun and protected from flooding are especially preferred as nesting sites. Many species prefer to nest in well-drained sandy soils or silty loams (Cane, 1991). Some nest in dense aggregations that persist for decades (Michener, 2000); others construct highly scattered ephemeral nests.

About 10 percent of North American bees nest in wood (Michener, 2000). Carpenter bees (*Xylocopa* spp.) have strong jaws to excavate extensive galleries in soft, dry, dead wood. Small carpenter bees (*Ceratina*), mason

bees (*Osmia* spp.), and some leafcutter bees (*Megachile* spp.) use cavities made by wood-boring cerambycid or buprestid beetles. Nesting female bees match the diameter of their bodies to evacuated natal tunnels of the beetles (Krombein, 1967). This nesting biology makes it possible to “trap nest” and collect numerous females of diverse species in the twig-nesting guild. Those species will readily build nests in blocks of wood that have been drilled with appropriate-sized holes (Gathmann et al., 1994; Krombein, 1967; Tscharrntke et al., 1998).

About 45 species of North American bumble bee nest principally in cavities within the ground. Upon emerging from diapause in the early spring, bumble bee queens seek rodent burrows, abandoned mouse nests, and other cavities in which to found their colonies and rear their first broods (Goulson, 2003c; Heinrich, 1979, 2004; Michener, 1974). In the southwestern United States, bumble bees (such as *B. sonorus*) often nest in or near human structures—under boards, in sheds, in walls, or even in abandoned mattresses or automobiles (S. Buchmann, unpublished data).

Once a nest is built, it can be modified by the addition of construction materials or glandular secretions. Ground-nesting bees typically use nothing more than exocrine gland secretions (Michener, 2000; O’Toole and Raw, 1991; Stephen et al., 1969). Bees that nest in pithy twigs, stems, or dead wood often forage at some distance from their nests for additional construction materials (Roubik, 1989). Pieces of foliage often are used by leafcutter bees (*Megachile* spp.) to form cell walls and end plugs. *Osmia* spp. often construct cell walls and end plugs from mud gathered nearby (Bosch and Kemp, 2001). Other *Megachile* species use resins, pebbles, and plant materials to form divisions between larval cells or to prevent entry to their nests by ants, parasitic wasps, or birds (Krombein, 1967; Michener, 2000; Stephen et al., 1969).

In agricultural plantings, where leafcutter and mason bees are used to pollinate crops, it can be necessary to provide patches of fresh mud (for *Osmia* spp. mason bees) or appropriate plants from which bees can cut leaves to form their cells. In the case of the introduced alfalfa leafcutter bee, alfalfa plants themselves provide pollen, nectar, and the leaves the bees use to create their nests. Other twig- or wood-nesting bees (such as *Xylocopa*) line their nests with layers of glandular exocrine secretions (Cane, 1991; Michener, 2000; Roubik, 1989). Social bees, including bumble bees, stingless bees (meliponines), honey bees, and some orchid bees (euglossines), use collected materials and beeswax secreted from their abdominal wax glands to build nests (Michener, 1974). Even for commercially managed bee pollinators, it can be necessary to provide supplemental sources of nesting materials.

Restoring, Managing, and Conserving Wild Bee Habitat

The plant resources required by bees for food and nesting dictate that strategies for maintaining healthy and diverse communities of pollinator populations must focus on conserving and restoring diverse plant communities (Forup and Memmott, 2005; Kremen et al., 2002a; Matheson et al., 1996; O'Toole, 1993, 1994). Providing sequences of blooming plants that encompass the entire flight period of the pollinator is one important component of maintaining pollinator populations, whether these series result from small-scale modifications on farm sites or in gardens or from large-scale regional restoration (Vaughan et al., 2004). Similarly, plans to provide habitat for bees or other pollinators (Table 6-2) must consider not only food resources, but also the specialized resources used for breeding, nesting, or overwintering.

Several factors should be considered in determining appropriate planting mixes. First, native plants are generally preferable to introduced species because they help maintain North American biodiversity of plants and pollinators (Shepherd et al., 2003). Ideally, plants are not just native to the continent but they are native to and genetically adapted to the region and to the site conditions (McKay et al., 2005). Second, plants must provide a complete phenological suite of resources for key pollinator species (Kremen et al., 2002a). Developing an optimal plant list requires research on the network of interactions between plants and pollinators and on which critical "bridging" plants might be needed to provide resources during periods of dearth (see, for example, Forup and Memmott, 2005; Kremen et al., 2002a). Finally, conserving existing original habitats generally should take priority over restoration, because restored habitats might not replicate every component that is functionally significant to pollinator species (Zedler and Callaway, 1999), and goals for restoration can be difficult to establish (Ehrenfeld and Toth, 1997).

Nesting Sites and Substrates

The alkali bee (Box 6-2), which has been successfully managed for pollination of alfalfa in the Pacific Northwest (Chapter 2), provides an example of how creation of supplemental or artificial nesting sites can enhance bee populations. Remarkably, few restoration ecologists have tested the efficacy of supplemental nesting sites for ground-nesting bees to enhance wild populations or to provide stable long-term habitat (but see Forup and Memmott, 2005). Investigating the effects of supplementation on nest occupancy, abundance, and persistence of wild bees is therefore a high priority for research.

BOX 6-2

Alkali Bee: Case Study in Managing a Ground-Nesting Commercial Pollinator

Nomia melanderi, the alkali bee, is native to arid areas west of the Rocky Mountains. It nests obligately in alkaline areas in California, Colorado, Idaho, Nevada, Oregon, Washington, and Utah. Before human colonization, alkali bees nested in dry lake beds and similar habitats, requiring soils with an alkaline surface crust of salt. The bees nest at depths of 8–16 cm in aggregations of as many as 240 bees per square meter (Bohart, 1958, 1967, 1972b; Cane, 2003). Alkali bees visit native legumes for pollen and nectar and are extremely efficient pollinators of alfalfa, for which they are managed as commercial pollinators. Today, specially prepared alkali bee nesting beds have been created in four states. In Washington's Touchet Valley the bee nesting beds average 6200 m²—the largest site had 1.7 million bee nests. In 1992, the cost per acre to pollinate alfalfa with alkali bees was estimated at \$30 (Willet and Gary, 1992).

Methods for creating appropriate nesting conditions for *N. melanderi* were developed and tested at the ARS Bee Biology and Systematics Laboratory in Logan, Utah (Cane, 2003). To create artificial nesting beds, prepared soil is moved into basins with underlying gravel or plastic and standpipes to create an upwelling of moisture to the surface. Salt is applied heavily to the soil surface to form a crust that mimics the salt pans and playas where bees nest naturally. Backhoes fitted with hydraulic punches remove block soil cores from existing nesting aggregations, and the cores are planted in new alkali bee beds to establish nesting sites adjacent to commercial alfalfa fields. Although moving nests and underground cells of ground-nesting bees is notoriously difficult and rarely attempted, it has worked well for establishing nesting aggregations of alkali bees in artificial nest beds. The bee beds are expensive initially, but once established they are sustained by the bees themselves. Maintenance costs are low and the beds last for decades.

In the 1960s and 1970s, alfalfa growers began to rely less on the native alkali bee for pollinating their crops (Mayer and Johansen, 2003) and shifted to using the alfalfa leafcutter (*Megachile rotundata*), an introduced species. The decline in the alkali bee industry probably was the result of pesticide use for controlling rangeland grasshoppers, competition from honey bees, and several rainy years, when the alkali bees' underground cells suffered unusually high mortality (Mayer and Johansen, 2003; Chapter 3). Although few managed alkali bee beds remain, new research and educational efforts are beginning to attract new practitioners to the field (Cane, ARS, personal communication, January 2006).

Ground Nesters

Suitable habitats, including open ground or vertical walls, ditches, or banks, can be created or modified within natural or anthropogenic habitats as bee nesting sites. For example, piles of sand have been used in Europe to create nesting substrates for bees (O'Toole and Raw, 1991). Some habitat manipulations are simple and compatible with human habitation in Mexico and the southwestern United States; solitary bees often nest within adobe walls, which are relatively inexpensive, available, and durable (Buchmann, unpublished data; Stephen, 2003).

Twig Nesters

Because wood-loving bees vary in size, nesting females choose tunnels of appropriate diameter and depth that have been vacated by the emerging adult wood-boring beetle (Buprestidae, Cerambycidae) (Linsley, 1958). Given that beetles and bees are ecological partners, actions to increase larval substrates for wood-boring beetle taxa can increase the availability of nest sites for pollinating bees and some wasps (Jones and Munn, 1998; Shepherd et al., 2003). Not all woods or plant species provide suitable nesting substrates. Generally, soft woods that are not colonized by fungi are preferred by guilds of wood-nesting bees (Krombein, 1967). Thus, retaining dead branches or trees is an essential part of habitat management for healthy bee populations and communities. Removing large amounts of dead wood for fire wood (mesquite, palo verde, and ironwood in the southwestern United States) results in the rapid elimination of many native bees (Buchmann and Nabhan, 1996; Buchmann, unpublished).

Bee nesting habitats also can be created by attaching drilled-board trap nests to fence posts, dead trees, or buildings (Griffin, 1999; Krombein, 1967; Shepherd et al., 2003). A balanced strategy of conserving beetle-infested dead trees and branches, setting out trap nests, and drilling holes into dead trees should increase local bee populations (Buchmann, unpublished). Detailed instructions for drilled-board trap nests are in the literature (Bosch and Kemp, 2001; Griffin, 1999; Krombein, 1967; Shepherd et al., 2003) and online (<http://snohomish.wsu.edu/mg/ombblock/ombblock.htm>; <http://www.nwf.org/backyardwildlifehabitat/beehouse.cfm>).

Cavity Nesters

Nest boxes made of wood or Styrofoam with plastic or rubber hose entrance tunnels can be provided for bumble bee species that nest underground. The boxes can be buried or nestled into bank or ditch sides to attract founding bumble bee queens in the spring. Adding upholsterer's cotton, abandoned mouse nests, or other nesting materials can improve the nests'

attractiveness (Heinrich, 2004; Intenthron and Gerrard, 1999). Nest boxes yield variable success that depends largely on the skill and knowledge of the builder and person placing the boxes in the field (Heinrich, 2004; Kearns and Thomson, 2001; Prÿs-Jones and Corbet, 1987). Extensive work on the chemistry of bumble bee pheromones has been conducted for some species (Bergström et al., 1996; O'Neill et al., 1991); the use of pheromone lures in the early spring to attract females to nest boxes could be useful although it has not yet been evaluated.

If colonies are started in the laboratory from wild-caught queens, their diet must be supplemented with pollen (often collected from *Apis* colonies using pollen traps) and sugar water or diluted honey. Colonies replaced to the wild should be kept away from areas where insecticides are sprayed, or spraying should occur at night when bees are inside their nests. Although established *Bombus* colonies can be purchased from commercial insectaries, they should not be used in reintroduction programs or as crop pollinators outside of greenhouses because of the possibility of transmitting pests and pathogens to local conspecifics or congeners (Colla et al., 2006).

Seeding Areas with Established Nests

Nests of wood or ground-nesting bees can be collected in natural habitats and introduced elsewhere to reestablish populations, although this approach is still experimental. Occupied branches or inhabited dead trees can be moved from one area to another to seed a new habitat with bees (Yurlina, 1998). Trees and nesting blocks were used in New Jersey at the Fresh Kills landfill to reintroduce native bee species to the active restoration site (Handel, 1997; Handel et al., 1994; Yurlina, 1998). Introductions of occupied nests, however, are more common in commercial agricultural pollination. Twig-, wood-, and cavity-nesting bees are generally more manageable than are ground-nesting bees (Bosch and Kemp, 2001). Several leafcutter and mason bee species are routinely moved in artificial domiciles to orchards and alfalfa fields for agricultural pollination (Chapter 1). Other than alkali bees (Box 6-2) (Bohart, 1958, 1962, 1972a; Cane, 2003), ground-nesting bees have been difficult to manage commercially as pollinators. There is not enough information available to determine whether reintroducing native twig-nesting bees into restored habitats would allow establishment or whether ground-nesting bees can be similarly reintroduced and established.

Agricultural Landscape Management

Floral Resources

Many of the options for increasing the diversity and abundance of floral resources on farms to accommodate the needs of a diverse pollinator

community (Batra, 2001; Bugg et al., 1998; Matheson, 1994; Pywell et al., 2006; Vaughan et al., 2004) do not necessarily reduce farming productivity, and they can even improve productivity by providing additional benefits beyond pollination services, such as nectar for natural enemies of crop pests (Pickett and Bugg, 1998). The options are listed here in order from the least expensive, most easily implemented to larger scale, more costly, or more complex changes.

- Growing polycultures rather than monocultures in a field results in a more diverse set of floral resources. Including flowers that bloom at different times of the year provides for and attracts a greater number of pollinator species, including those with long flight seasons.
- Tolerating weeds along crop borders can provide a diverse and abundant set of floral resources, at no cost to the farmer.
- Insectary strips planted within crop fields or in field margins and in buffer strips provide abundant pollen and nectar sources and attract bees to the fields (Altieri and Nicholls, 2004; Carvell et al., 2004; Pywell et al., 2005).
- Planting cover crops on resting fields or as orchard understory and allowing cover crops (such as clovers) to bloom before plowing them under provides “green manure” that benefits both pollinators and soil fertility.
- Planting wildflower mixes in fallow or old fields or allowing weeds to colonize creates meadows that support pollinators as the fields rest.
- Planting permanent hedgerows of native perennial forbs and shrubs provides nest sites and preferred pollen and nectar sources for a diverse community of pollinators in the spaces between fields. Such hedgerows may also serve as wind-breaks or provide erosion control.
- Restoring natural habitat patches on farms in permanent set-asides—focusing on areas that are more difficult to farm, such as edges of ditches, ponds and riparian areas, on hills, or around utility poles—can provide undisturbed habitat for pollinators.

Some governments, particularly in Europe (Box 6-3), have developed extensive monetary incentives to encourage environmental stewardship by farmers and ranchers. They include promotion of fallow and set-aside programs, as well as the planting of annual or perennial wildflowers for forage for pollinators along field margins and between fields. Among the specialty seed mixes of local wildflower species that have been developed in Europe is the “Tübingen mix,” which is in wide use in Europe (Engels et al., 1994; Matheson, 1994). Monitoring programs have demonstrated that integrating low-cost pollen and nectar sources into field borders provides measurable improvements in abundance and richness of several pollinator groups (Carvell et al., 2004; Pywell et al., 2004, 2006). The increase in land-

BOX 6-3

EU Biodiversity Conservation in Agriculture

The European Union (EU) and most of its member states have set a target of halting the loss of biodiversity by 2010. Detailed EU-sponsored research programs provide the scientific rationale for policy development (including the ALARM program [Chapter 5] and the SAFFIE project). Several policy instruments are available (agri-environment schemes and biodiversity action plans) to provide incentives for implementation.

Science Programs

ALARM, or Assessing Large Scale Environmental Risks to Biodiversity with Tested Methods is funded by the European Commission under Framework 6. The overall research program has several aims:

- Quantify distribution shifts in key pollinator groups across Europe.
- Measure biodiversity and assess economic risks associated with the loss of pollination services in agricultural and natural systems through the development of standardized tools and protocols.
- Determine the relative individual and combined importance of drivers of pollinator loss (land use, climate change, fertilizer and pesticide contamination, invasive species, socioeconomic factors).
- Develop predictive models for pollinator loss and consequent risks (Settele et al., 2005). ALARM has 54 EU partner institutions working in a 5-year, 22-million-euro project (2004–2009; Box 2-3, Box 5-1).

SAFFIE, Sustainable Arable Farming for an Improved Environment, is a United Kingdom research program designed to sustain the management of arable farms to support more wildlife. Its main objectives concern testing methods for enhancing farmland biodiversity. Farmers are encouraged to use alternative approaches to habitat management of crop and field margins as a way to develop more sustainable farming. The project has 20 partners and £3.5 million in funding over 5 years (2002–2007).

Policy Instruments

Agri-environmental schemes provide programs that encourage EU farmers to carry out environmentally beneficial activities on their land. The aim is to enhance biological diversity in a range of plant and animal groups, including pollinators. Farmers recover the cost of supplying environmental services through government payments. Examples of activities include the following:

- Reversion of intensively used land to biologically diverse but less profitable extensively farmed land
- Reductions in nutrient use
- Reduction or cessation of pesticide use (such as through organic farming)
- Creation of nature zones from lands removed from production
- Continuation of traditional environmental land management in zones liable to neglect

- Maintenance of landscape features that are no longer agriculturally viable

The programs are managed by regional or national authorities under a decentralized system, subject to approval by the European Commission. The costs are partly financed by the EU. Fifteen member states are operating agri-environmental programs that cover 900,000 farms and 27 million hectares, about 20 percent of EU farmland (for information on EU, visit http://www.europa.eu.int/comm/agriculture/envir/index_en.htm; for information on its member states visit http://www.europa.eu.int/comm/agriculture/rur/countries/index_en.htm).

The agri-environment schemes in various European countries have yielded mixed, taxon-specific results. Although positive results have not been demonstrated for all taxa studied (Kleijn et al., 2001, 2004), some pollinator groups, notably bees, butterflies, and flower flies, appear to benefit in some cases (Carvell et al., 2004; Kleijn et al., 2001, 2004, 2006; Pywell et al., 2005, 2006; Weibull et al., 2003). Scientific monitoring of the schemes, particularly before-after control-impact monitoring (Potts et al., 2006), is critical to assessments of effectiveness, and much can be learned and applied from the work in Europe.

The United Kingdom operates four optional agri-environmental schemes (U.K. Department of Environment, Food and Rural Affairs, 2002) that pay farmers to practice environmentally friendly farming. The Countryside Stewardship Scheme aims to conserve, enhance, and restore target landscapes. The Organic Farming Scheme facilitates the shift from conventional to organic farming. The Environmentally Sensitive Areas Scheme covers 22 specific areas of national environmental significance.

The Entry Level Agri-Environment Scheme is a new program that is expected to include more than 70 percent of British farms. The intention is to promote simple, effective environmental management to enhance farmland biodiversity across a range of plant and animal groups, decrease diffuse pollution, maintain landscape structure, and conserve the historic environment. The program has several areas that promote pollinator biodiversity according to replicated field experiments (Carvell et al., 2004; Pywell et al., 2004, 2006):

- Field margins sown with buffer strips provide forage (nectar and pollen) and nesting resources for pollinators and safeguard boundary habitats against chemical sprays.
- Grasslands sown with mixes that include pollen-and-nectar flowers can increase the diversity, abundance, and availability of forage resources, and increases bumble bee diversity and abundance.
- Careful management of hedgerows can create and protect habitats suitable for pollinators.
- Permanent grasslands can be established with very low input to provide long-term pollinator habitat.

SOURCE: <http://www.defra.gov.uk/erdpschemes/default.htm#land>.

scape heterogeneity that accompanies these methods also can be beneficial (Tschardt et al., 2005).

The U.S. federal government also offers incentives through the Farm Bill, which is administered by USDA's Natural Resource Conservation Service (NRCS). This agency maintains and offers state lists of approved or suggested plants for revegetation (in buffer strips or for hillside erosion control) or for seeding rangelands for cattle production (<http://www.nrcs.usda.gov/>; <http://plants.usda.gov/>). Some recommended species are potentially invasive exotic plants or are grasses that provide little or no floral reward for bees and other pollinators. In some cases, most notably the new Conservation Security Programs, pollinator-friendly plants are specifically recommended (USDA-NRCS, 2004, 2006a,b). More work is needed to develop appropriate lists of plants that support pollinators and to customize those lists for different ecoregions within North America.

Nesting Substrates

Methods also are available for providing or protecting nest sites and substrates for bee species in the agricultural landscape (Matheson, 1994; Vaughan et al., 2004); many of them do not interfere with farming. They range from simple, low-cost measures to more complex and expensive methods:

- Management of irrigation to preserve ground-nesting bees. By using drip or spray irrigation instead of flooding, farmers can avoid drowning ground-nesting bees and larvae. Interference with foraging and nest cell provisioning can be avoided by irrigating at night.
- Management of tillage to protect existing bees' nests. By shallower tilling or using no-till agriculture, disturbance of nest sites can be avoided. The density of squash bees (*Peponapis pruinosa*) on squash and pumpkin farms in the eastern United States that practice no-till agriculture is three times that of tilled farms (Shuler et al., 2005).
- Active land management to provide nesting sites for bees. Examples include creating patches of bare ground for ground-nesting bees within perennial plantings, such as hedgerows, or mowing or weeding within pastures; leaving dead wood and standing snags, drilling holes in dead wood, and putting out trap nests for twig-nesting bees; providing a sand-loam mix for ground-nesting bees; putting out bumble bee nest boxes, buried or above ground; and creating specialized conditions for nesting aggregations (Box 6-2). More research is needed to determine which active management techniques are most effective for pollinator conservation and to adapt them for different bee faunas and site conditions.

Alternatives to Chemical Pest Controls

According to the National Center for Food and Agricultural Policy, more than 68 active ingredients are used to control insect pests on North American farms (<http://www.ncfap.org/whatwedo/index.php>). Insecticides are differentially toxic to nontarget species, depending on the active ingredients, the strength and composition of the formulation (dust, powder, liquid), and the behavioral and physiological response of the target insect (Johansen, 1977; Johansen and Mayer, 1990). Some pollinator species might not be killed outright by pesticide applications, but they could suffer sublethal effects, including reduced foraging ability, that ultimately hamper their productivity (Morandin et al., 2005; Vaughan et al., 2004).

Short of eliminating insecticide use altogether, growers can reduce risks to pollinators from pesticides in several ways (Johansen and Mayer, 1990; NAPPC, 2006; Vaughan et al., 2004):

- Choose appropriate pesticides. Some insecticides have active ingredients that are less likely to cause mortality or sublethal effects in bees, to have formulations that are less toxic to bees (for example, granular powders are less noxious than dust; Johansen and Mayer, 1990), and to break down more rapidly than others do. Microencapsulated formulations should be avoided because they mimic pollen.
- Apply pesticides selectively. Growers can avoid using insecticides during a crop's bloom period, apply them at night while bees are in nests, and apply them on the ground rather than in aerial spray.
- Convert some or all fields to organic production. Growers thus provide areas that are refuges from pesticides (Vaughan et al., 2004).

Grassland and Grazed Land Management

Natural grasslands (prairies) are now considered the rarest North American biome; more than 90 percent of the continent's grassland area is now in agricultural use, and 14 of the 16 temperate grassland, savanna, or scrub ecoregions in North America are classified as either critical or endangered (Ricketts et al., 1999). The loss involves more than grasses; annual wildflowers and perennial plants are important vegetative components of grassland biomes. Flowering plant, arthropod, and vertebrate biodiversity is often higher in grasslands than in other North American biomes (Butaye et al., 2005; WallisdeVries et al., 2002).

Management of prairies and grazed lands includes mowing, grazing, or prescribed burns that can either harm or benefit pollinators (Carvell, 2002; Potts et al., 2003; Rathcke and Jules, 1993; Smallidge and Leopold,

1997). Plans for managing pollinator populations and communities also must consider the effects of invasive species on the composition of natural vegetation. Specific practices that provide nest sites for pollinator species might need to be considered for management protocols.

Mowing or Grazing

Many butterflies and other insects depend on habitats in early succession (Smallidge and Leopold, 1997), and mowing or grazing can be essential to maintaining the early successional habitat types as patches within the landscape, particularly if organisms that formerly grazed there (such as bison) are now missing. In habitats where fire is the natural agent of disturbance, mowing or grazing can be more beneficial to the maintenance of pollinator habitats, particularly if habitat patches are small and isolated. In particular, pollinator species of interest suffer some larval or adult mortality from fire (Smallidge and Leopold, 1997). Mowing at the appropriate time (August) is also a good method for maintaining early successional patches for the endangered Karner blue butterfly (*Lycæides melissa samuelis*) and its lupine host plant (*Lupinus perennis*) within sandy pine barrens, pine-oak savannahs, and oak savannahs in the Great Lakes region. Mowing also allows new patches to be localized within the dispersal limits of the butterfly, permitting colonization from nearby occupied patches of lupine (Smallidge and Leopold, 1997). Recent grazing was linked to increased bumble bee richness and abundance in calcareous grasslands. In the United Kingdom, grazing probably contributed to bumble bee abundance by enhancing diversity and the abundance of forage plants preferred by bumble bees and by reducing vegetation height, canopy closure, and moss litter (Carvell, 2002).

Burning

Fire can cause mortality in pollinators that nest above ground (larval and pupal lepidopterans and twig-nesting bees) and lead to reductions in abundance (Smallidge and Leopold, 1997). Most ground-nesting bees, however, nest at a soil depth of more than 5 cm (Michener, 2000), so the soil could insulate the nests and reduce or eliminate mortality from wildfires or prescribed burns.

In fire-adapted communities, many plants require fire or heat to open fruits or scarify seeds (for example, Givnish, 1986). Such communities often respond to a fire with abundant new growth, including annual wildflowers, plants from bulbs, or regenerated sprouts. The flush of postfire vegetation often produces an equally dramatic spike in nectar and pollen for local pollinators; one example is fireweed, *Epilobium* spp., in the eastern United States (Heinrich, 2004).

From a site in Israel that had high pollinator biodiversity (Mt. Carmel), Potts and colleagues (2003) discovered that fire initially was catastrophic to plant and bee communities, but that recovery was rapid. Within 2 years of the fires there was a peak in plant and bee diversity that was followed by a long and steady decline over the next 50 years. They reported that bee pollinator communities closely matched the plant community in recovery and regeneration (Potts et al., 2001, 2003).

Like mowing and grazing, fire is an important management tool that can be used to reset the successional sequence and maintain the diverse and heterogeneous mosaic landscapes that include early successional stages (oldfields) and late primary stages (climax forests). Resetting the successional sequence provides resources for a wider array of species (Pickett and White, 1985; Smallidge and Leopold, 1997). More information is needed on the short- and long-term effects of fire—and its use as a management technique—on diverse North American plant and pollinator communities.

Nesting Habitat

Although solid expanses of grasses and forbs are not productive nesting habitats for bees, they do provide nest sites (larval host plants) for a variety of Lepidoptera. Thus, grassland management protocols that are well adapted for Lepidoptera also should consider provisions for bee-nesting sites. Nesting sites can be provided by creating patches of bare ground or sand-loam mixes for ground-nesting bees; by maintaining a landscape mosaic of wooded and grassy areas, protecting some dead wood and standing snags and drilling holes in some dead wood; putting out trap nests for twig-nesting bees; and putting out bumble bee nest boxes, buried or above ground (Box 6-4). Large-scale herbicide applications, such as are applied in the southwestern United States to remove undesirable scrub and brush (mesquite and *Prosopis* plants), should be discouraged because they remove not only nesting sites and refuges, but also pollen and nectar sources for native bees, honey bees, and other pollinators (Buchmann and Nabhan, 1996).

MAINTAINING POLLINATION SERVICES

Maintaining commercial pollinator stocks and the diversity of wild pollinator communities differs from maintaining pollination services provided by pollinators, because pollination services could be enhanced without an increase in pollinators. This section presents strategies for maintaining pollination services to crops by commercial pollinators and pollination services to crops and wild native plant populations by wild pollinators.

BOX 6-4

Golf Courses and Other Urban and Suburban Green Spaces

Traditionally, golf courses have been inhospitable areas for pollinating birds, bats, and insects because of the large amounts of fertilizers, herbicides, and pesticides used and their close-cropped mowing. The U.S. Golf Association has adopted pollinator-friendly practices (Shepherd, 2002; Shepherd and Tepedino, 2000; Shepherd et al., 2001) for out-of-play areas (roughs), where wildflowers are planted, nesting domiciles (drilled bee boards) are provided, and few or no pesticides and herbicides are applied. Some golf courses have combined to form an association of organic golf courses (http://www.usga.org/turf/green_section_record/2005/jan_feb/Inorganic.html; <http://www.epa.gov/opbppd1/PESP/strategies/2005/ogmd05.htm>).

Similar techniques could be applied in urban parks and greenbelts, on large corporate campuses, and at a smaller scale in home gardens, to improve habitat for pollinators in urban and suburban areas. The abundant floral resources in backyard gardens in some urban areas already support diverse communities of bees and nest sites for twig-nesters in wooden fences or houses (Cane et al., 2006; Frankie et al., 2005).

Commercial Pollinators

Crops that require or are improved by animal pollination benefit from the services of commercially managed honey bees or other commercially managed bees. The supply of commercial honey bee colonies can be stabilized by reducing bees' vulnerability to pests, parasites, pathogens, and pesticides. If honey bee colonies are in short supply, a new and potentially useful compensation is to increase the available colonies' efficiency. Honey bee brood pheromones have been identified that temporarily increase the proportion of a colony's foragers that collect pollen (Pankiw, 2004). Hormone manipulations also can advance the age at which bees switch from working in the hive to foraging and increase the proportion of a colony's foraging-worker force (Robinson and Ratnieks, 1987). These pheromones and hormones could be developed into slow-release stimulants to increase a colony's pollinator force in a grower's field, although possible negative effects on bee hives also should be explored. The supply of alternative commercial pollinators requires caution to reduce losses to pathogens and parasites, as happened to the alfalfa leafcutter bee, for example. Intensified research and technology transfer will be required for development of new species of alternative pollinators.

Commercially managed pollinators can be brought to the crops that need their services, ensuring service delivery. Thus, growers of commodities that require pollination follow recommendations for pollinator stocking. For example, hybrid sunflower production requires two colonies of honey bees per hectare (Delaplane and Mayer, 2000). Although some improvements could be made to maximize benefits by altering the spacing of colonies in fields and the spacing of self-incompatible cultivars (Chapter 4), in general, the great advantage of using commercially managed pollinators is that service delivery can be controlled, or at least manipulated, by relative placement of pollinators and cultivars.

Wild Pollinators

It is far more difficult to ensure that services from wild pollinators are delivered to crops. Because the mechanisms are not still well understood, managing wild pollinators requires a better understanding of foraging ecology and population biology and how they are influenced by landscape properties (Kremen and Ostfeld, 2005). The few existing studies, however, suggest that healthy (diverse and abundant) pollinator communities could provide enhanced pollination services for a wider array of crops, and ensure stability of services within seasons and across years (Klein et al., 2003; Kremen and Chaplin, in press; Kremen et al., 2002a).

Because pollinators are mobile and they collect resources within the foraging range of a nest, roost, or territory (for example, hummingbirds), environmental qualities of the immediate site (local) and the surrounding area (landscape) affect their population sizes, densities, and persistence. Many pollinator species use a variety of floral and nesting resources that can be distributed across different habitat types at different times of the year (Westrich, 1996). Some pollinators use native plant resources that occur only in natural habitats in season, and weedy resources that occur in agricultural habitats in the summer (Kremen et al., 2002a). Mass-flowering resources provided by crops can also be important for selected species in a landscape (Westphal et al., 2003).

Evidence suggests that the character of a landscape is important in determining the richness, abundance, and composition of pollinator communities on farms. Pollinator species differ in their ability to provide services to different crops (for example, Free, 1993; Kremen et al., 2002b), and their effectiveness could vary with the community context in which they exist (Greenleaf and Kremen, 2006b; Thomson and Goodell, 2001; Thomson and Thomson, 1992). Therefore, alterations in the composition of pollinator communities due to landscape change influence both the quantity and quality of pollination services to crops—although local site characteristics also influence pollinator communities and services (reviewed in Kremen

and Chaplin, in press). In California's Mediterranean climate environment, landscape factors (the proximity or proportional area of natural habitat within a site) are the dominant factors for pollinator richness, composition, abundance, and services (Greenleaf, 2005; Greenleaf and Kremen, 2006b; Kremen et al., 2002b, 2004), although site characteristics (conventional or organic management of farm sites) modulate these responses at the population level (Kim et al., 2006; Williams and Kremen, in press). In tropical rainforest biomes of Central and South America and Indonesia and in temperate grassland biomes in Germany and Canada, pollinator richness, abundance, and services also respond primarily to proximity to natural or seminatural habitat at the landscape level (Chacoff and Aizen, 2006; Klein et al., 2002, 2003a; Morandin and Winston, 2005; Ricketts, 2004; Ricketts et al., 2004; Steffan-Dewenter and Tschardt, 1999; Steffan-Dewenter et al., 2001, 2002), but local factors, such as light (Klein et al., 2002, 2003b) and the abundance and richness of weedy floral resources (Morandin and Winston, 2005), also have statistically significant effects.

Pollination services for wild plants that depend on or benefit from animal pollination are generally provided exclusively by wild pollinator populations, although managed honey bees often forage on wild plants and, thus, provide some services (Kremen et al., 2002). Managing wild pollinator communities is needed to ensure pollination function for natural plant communities. Pollination services to wild plants in habitat fragments can be influenced by the size and isolation of the fragment, the characteristics of the surrounding human-modified matrix, and the resulting population responses of plants and pollinators (Bronstein, 1995; Ghazoul, 2005c). Small fragments tend to have small plant populations (MacArthur and Wilson, 1967), which can be less attractive to pollinators (Brody and Mitchell, 1997; also reviewed in Kunin, 1997), and thus become pollinator limited (Box 4-1; Groom, 2001). Smaller fragments often also contain smaller populations and fewer pollinator species (MacArthur and Wilson, 1967; Miller et al., 1995; Ricketts, 2001; Steffan-Dewenter, 2003) thus reducing pollinator visitation (Aizen and Feinsinger, 1994; Cresswell and Osborne, 2004). Empirical studies, however, have revealed positive, negative, and neutral effects of fragment size on pollinator abundance, richness, and services (Aizen and Feinsinger, 1994; Cane et al., 2006; Danielsen et al., 2005; Miller et al., 1995; Tonhasca et al., 2002; Winfree et al., 2006). The variability in response is probably attributable to differences in habitat specificity and dispersal ability among pollinator species (Law and Lean, 1999; Saville et al., 1997; Steffan-Dewenter, 2003).

Geographic isolation also can affect pollination services to wild plants (Ghazoul, 2005c). Plant populations in isolated fragments could be self-limited by the amount of compatible pollen available (Duncan et al., 2004). Isolated fragments contain smaller populations and fewer pollinator and

plant species (MacArthur and Wilson, 1967) thus reducing pollinator visitation and fruit set (Cunningham, 2000; Steffan-Dewenter and Tschardt, 1999). Corridors that link habitat fragments have been shown to increase movement of selected pollinator species and enhance pollination of target plants (Tewksbury et al., 2002; Townsend and Levey, 2005). Isolation also can reduce pollinator visitation and seed set (Jennersten, 1988), but in some cases, even highly isolated plants are known to receive sufficient out-crossed pollen to reproduce (Nason and Hamrick, 1997; Schulke and Waser, 2001; White et al., 2002).

All of the fragment-specific factors are likely to be modulated by the type of human-dominated matrix that surrounds natural fragments (Ricketts, 2001). If the surrounding matrix is hospitable to wild plants (Mayfield and Daily, 2005) or contains nesting or floral resources for some pollinator species (Klein et al., 2002; Westphal et al., 2003), the effects of fragment size and isolation can be alleviated. Relatively few studies of pollinator communities and pollination function in fragmented landscapes consider matrix effects (Cane et al., 2006; Dauber et al., 2003; Hirsch et al., 2003; Steffan-Dewenter et al., 2006; Williams and Kremen, in press; Winfree et al., 2006).

Clearly, managing landscapes and sites will be important for restoring, preserving, or maintaining diverse pollinator communities and ecological service functions to crops and wild plants. How much natural habitat is sufficient in the landscape for pollinator maintenance is an open question. Kremen and colleagues (2004) observed a log-linear relationship between the amount of pollination services provided to a watermelon crop and the proportional area of natural habitat within several kilometers of a farm. Full pollination services could be provided by wild bee communities at 30 percent or more natural habitat cover. Morandin and Winston (2006) determined that removing 30 percent of land from canola seed production would actually increase profits to canola farmers, because of the resulting increased diversity, abundance, and services provided by wild bees. Ricketts and colleagues (2004) suggested that fragments of at least 20 hectares of tropical rainforest provide valuable services to coffee from wild bees that are comparable to other land use values. Equivalent studies of native plants in natural habitat fragments are lacking.

How patches of habitat should be configured to deliver pollination services into the surrounding agricultural matrix (in the case of crops) or to maintain gene flow and population persistence for isolated populations of wild plants that are confined to fragments also is poorly understood. If wild pollinators in an area indeed depend on natural habitat fragments for nesting sites and critical floral resources, then crop pollination can benefit from a “service halo” around the habitat fragment corresponding to the foraging ranges of individual pollinator species (Ricketts, 2001; Ricketts

et al., 2004). Dispersing small fragments extensively throughout an area seems logical but leaves open the question of how to configure large parcels to allow pollinator populations to persist. Both metapopulation theory (reviewed in Hanski and Ovaskainen, 2000; Harrison and Fahrig, 1995) and empirical data (Harrison et al., 1988) suggest that some larger patches are needed to support larger sized populations that are more resistant to extinction (see also Berger, 1990; Zayed and Packer, 2005). Larger areas also will, in theory, contain more diverse assemblages of pollinators (MacArthur and Wilson, 1967; Simberloff and Wilson, 1969) that might provide more services, more consistently, and contribute to pollination of a wider variety of crops (Kremen and Chaplin, in press) and other plants (Memmott, 1999; Memmott et al., 2004). More research is needed to determine the optimal configuration of landscape fragments and their connectedness to maintain pollinator populations, communities, and functions.

PUBLIC POLICY AND POLLINATOR POPULATIONS

U.S. Endangered Species Act

The Endangered Species Act (ESA) of 1973 is the broadest and most powerful U.S. law for the protection of endangered species and their habitats (NRC, 1995). The act lists species of plants and animals (vertebrate and invertebrate) as *endangered* or *threatened* according to assessments of their risk of extinction (Congressional Research Service [CRS], 2006). Once a species is listed, ESA's strict substantive provisions become legal tools to assist in the species' recovery and the protection of its habitat. Endangered species and their critical habitats are entitled to strong protections. It is illegal, for example, to take any endangered species in the United States or its territorial waters, and any federal action that will jeopardize the future of an endangered species is prohibited, including any action that threatens to destroy or damage critical habitat. At press time for this volume, in the fall of 2006, 1879 U.S. and foreign animals and plants were listed as endangered or threatened (U.S. Fish and Wildlife Service [USFWS], 2006).

ESA's major goals include the recovery of endangered and threatened species to the point at which protection is no longer needed. As this volume went to press, USFWS (2006) had cataloged 17 U.S. and foreign species that had been recovered and removed from the list. The populations of other listed species have increased, and some appear to have stabilized even though they remain on the list.

A species is placed on the Endangered Species List on the initiative of the secretary of the interior or of the secretary of commerce. The decision is based on the best available scientific and commercial information and a

lengthy procedure that ensures public participation and the collection of relevant information. Because Congress directed that listing have a scientific foundation for the label of *threatened* or *endangered*, economic factors are not considered in the listing decision. In June 2006, there were 282 “candidate” species for which no decision had been made. The status of those species is to be monitored and, if any emergency poses a significant risk to their continued existence, they must be listed promptly.

Modifications of ESA and other recently proposed changes could make it more difficult to list pollinators than some other animals. A 1981 congressional revision specifically exempted any “species of the Class Insecta determined by the Secretary to constitute a pest whose protection under the provisions of this Act would present an overwhelming and overriding risk to man.” Any species that has caused economic damage or could do so is less likely to be protected. The larvae of some lepidopteran pollinators, for example, and the adults of some hymenopteran pollinators can under some circumstances cause economic damage. Securing endangered status for them could prove problematic.

Recent efforts to amend ESA also could add new barriers to listing pollinators. H.R. 3824, passed by the House of Representatives in 2005, “To amend and reauthorize the Endangered Species Act of 1973 to provide greater results conserving and recovering listed species, and for other purposes” replaces the criterion of “best scientific and commercial data available” with “best available scientific data.” More important, unlike ESA itself, H.R. 3824 for the first time defines “best available scientific data” as “scientific data, regardless of source, that are available to the Secretary at the time of a decision or action for which such data are required by this Act and that the Secretary determines are the most accurate, reliable, and relevant for use in that decision or action.” The secretary is directed to issue regulations that establish criteria for “best available scientific data” and must ensure that the information consists of empirical data or data found in sources that have been subjected to peer review by people recognized by the National Academy of Sciences [NAS] as qualified to independently review a covered action in a manner that is in compliance with the Data Quality Act (44 USC 3516) (Congressional Research Service, 2006). According to CRS, “Some contend that the specification of empirical data in H.R. 3824 would exclude estimates derived from models and limit the type of data available for use. . . . However, estimates derived from modeling could be allowed under H.R. 3824, if it meets the NAS peer-review conditions set forth in the bill.” Because of the paucity of data available for many pollinator species (Chapter 2), assessments of species status often are based on information derived from population models or from genetic studies, which could be excluded if ESA is amended as proposed.

Incentives for Stewardship

The public benefits provided by wild pollinators justify public policy that encourages stewardship of wild pollinators. Given the importance of habitat, land stewardship policies constitute the majority of relevant mechanisms. However, consumer-oriented measures also have a role in pollinator conservation policies.

For agricultural lands, there are four voluntary programs that can be used or adapted to create or maintain pollinator habitat. The Farm Security and Rural Investment Act of 2002 (the Farm Bill) authorized them:

- The Wildlife Habitat Incentives Program (WHIP) (NRCS, 2006a) provides cost sharing and incentive payments to eligible farmers for planting native and nonnative plants that could enhance wildlife habitat (including pollinators) through early successional habitat development, riparian herbaceous cover, tree and shrub establishment, and upland and wetland habitat management.
- The Environmental Quality Incentives Program (EQIP) (NRCS, 2006b) also provides money to eligible farmers who focus on soil and water conservation. The program can be customized to include pollinator habitat through improvements in hedgerows, riparian buffer strips, tree and shrub planting, and wildlife habitat management.
- The Conservation Reserve Program (CRP) (USDA-FSA, 2006) pays eligible farmers to convert agricultural land to conservation uses under a 10-year contract. Farmers make bids that describe their land management plans and the annual payments they would require. The Farm Service Agency (FSA) evaluates the bids in light of technical advice from NRCS. The evaluation is based on state priorities, and points are awarded for expected conservation benefits from plans that include native species, especially flowering shrubs and forbs. Currently, no points are assigned explicitly for pollinator habitat.
- The Conservation Stewardship Program (CSP) (NRCS, 2006c) awards 10-year contracts to eligible farmers according to the farmers' proposed intensity of stewardship and their proposed practices. CSP payments for pollinator habitat are available as "resource enhancements" under the rubric of "wildlife habitat management." In 2005, North Dakota's state NRCS program covered pollinator habitat under three CSP enhancements involving native herbaceous cover plots, unharvested tame hay land, and native woody cover plots (NRCS-North Dakota, 2005).

WHIP, EQIP, and CRP are available to farmers who have traditionally raised wheat and feed grains eligible for federal price supports. Because of the tightening federal budget, access to payments for conservation practices is rationed through priorities established by state technical committees and

according to the characteristics of individual conservation plans submitted by landowners. Many states do not assign points for enhancing pollinator habitat or provide guidance for doing so. In the states that do provide points, such as Michigan, very few landowners had enrolled as of December 2005. CSP eligibility is further restricted to farmers in a limited number of watersheds in each state on a list that rotates annually, with the goal of making each watershed eligible every 7–10 years (A. Herceg, NRCS, personal communication, December 2005).

Although the four U.S. farm environmental stewardship programs provide a sound vessel for encouraging landowners to enhance pollinator habitat, interest among farmers has been limited. The research base for NRCS to estimate the on-farm and external conservation benefits from pollinator habitat also is limited. Development of a national monitoring program for pollinator species would provide a remedy (Chapter 5).

For nonfarm, private landowners—homeowners, public utilities, or businesses—investments in pollinator habitat could be encouraged through income tax deductions. Public agencies involved in land management, such as the U.S. Forest Service, the U.S. Department of the Interior, and the U.S. Department of Transportation, could include provisions for pollinator protection or enhancement in their guidelines. The inclusion of pollinator protection in the criteria for federal land leases for grazing and timber harvest also could encompass large areas of land. Some interstate highways already have wildflower plantings, which could be enhanced by purposeful selection of appropriate native plant species favored by wild pollinators.

Volunteer networks also could encourage creation or restoration of pollinator habitats much as they have done for pollinator monitoring in the Audubon Society's annual Christmas Bird Counts and the North American Butterfly Association's Fourth of July counts (Chapters 2 and 5). Monarch Watch's Monarch Waystation program has already resulted in the creation and registration of more than 600 butterfly-friendly habitats with nectar resources and host plants. A private, nongovernmental organization interested in pollinators might establish a "friends of pollinators" network that could be diffused through school programs and public service announcements. Interest could be sparked through activities such as a landscape architecture competition for designs that invite and support pollinator populations.

Even consumers can engage in pollinator protection. Following the successful ecolabeling campaigns for dolphin-safe tuna and shade-grown coffee, a label could be used to certify pollinator-safe fruits and vegetables. With the important exception of the USDA organic label, most food certification labelling is done by private organizations. Currently, however, there are no known organizations that are both interested in and capable of developing and providing certification for a pollinator-protector label.

ADAPTIVE MANAGEMENT AND POLLINATOR MONITORING

Different management strategies can be used across landscapes, including public and private lands, working lands, and natural areas, to improve conditions for pollinators and to maintain pollination function in crops and wild plants. Strategies range from site-specific management that could be performed by private landowners, to landscape and regional actions that would require coordination by county, state, or regional authorities and nongovernmental organizations. Although management actions can be guided by a body of existing scientific knowledge, all are experimental; therefore, concurrent monitoring of pollinator status and of pollination function is needed (Chapter 5) to determine the efficacy of different strategies and to adapt measures to provide even better performance (Kremen et al., 1993; Margoluis and Salafsky, 1998; Walters and Holling, 1990).

CONCLUSIONS

This chapter presents various actions that could be taken to maintain commercial pollinators, wild pollinator species and communities, and pollination function. The committee suggests the following as priorities.

Apis

- Develop and refine both traditional and molecular methods for identifying bees with economically desirable traits for inclusion in honey bee breeding programs.
- Select model populations of honey bees with economically desirable traits for adoption by the beekeeping industry.
- Develop educational materials and programs to enable private-sector queen producers to develop and maintain pest, parasite, and pathogen resistant stocks of honey bees and to serve as reliable sources of quality production queens that produce colonies expressing useful levels of economically important traits.
- Develop sustainable methods for ensuring that Africanized bees do not degrade the commercial value of existing stocks of honey bees.
- Develop resistance management programs to mitigate the adverse effects of pesticide and antibiotic resistance in honey bee pest, parasite, and pathogen populations.
- Develop methods for the preservation of honey bee germplasm.

Other Commercial Species

- Identify commercially viable solutions to the problem of chalkbrood in the alfalfa leafcutter bee, *Megachile rotundata*.

- Identify non-*Apis* bees with the potential to be developed into economically useful pollinators.
- Develop commercially viable methods for culturing economically important species of bumble bees and solitary bees for use as crop pollinators.

Wild Bees

- Inform the public—in particular, the agricultural community and managers of golf courses, urban parks, and other large urban-suburban areas such as industrial and academic campuses—about current knowledge of actions (such as creating pollinator habitat) that can be taken to manage pollinators.
- Conduct field studies in different regions of North America to determine the suites of key floral resources for use in restoration protocols in each region.
- Conduct additional studies that can be used to improve existing restoration protocols, including monitoring the influence of restoration activities on population and community dynamics of pollinators and understanding land managers' willingness to adopt restoration practices.
- Define land-management practices (by NRCS state offices) that encourage pollinator populations that are eligible for federal payments under existing Farm Bill conservation programs such as EQIP, WHIP, CRP, and CSP.
- Integrate land management practices that encourage pollinator populations at the state level into existing Farm Bill conservation programs such as EQIP, WHIP, CRP, and CSP.
- Conserve existing natural habitats in human-dominated landscapes.

Findings and Recommendations

The Committee on the Status of Pollinators—a group of 15 academics, museum-based systematists, and representatives of nongovernmental organizations—convened in July 2005 and received a set of specific questions to address:

- Are pollinators experiencing serious decline, and if so, to what degree?
- What research and monitoring are needed to provide improved information?
- In cases where decline can be established by available data, what are its causes and how can they be addressed?
- What are the potential consequences of decline in agricultural and natural ecosystems?
- What conservation or restoration steps can be taken to slow, reverse, or prevent pollinator decline?

The committee was asked to compile and analyze the published literature, determine the state of knowledge on pollinator status, identify knowledge gaps, and establish priorities for addressing these gaps. This chapter provides the committee's recommendations as they relate to each question in the statement of task. The recommendations are aimed at improving documentation of population trends and monitoring declines, addressing the causes of decline, developing methods of stopping or reversing declines, and prioritizing research for preventing future declines.

The value of determining the status of North American pollinators

became abundantly clear in short order. More than three-quarters of angiosperm plant species rely on animals for pollination. Although most major food grains are wind-pollinated grasses that do not require services of animal pollinators, most fruits and vegetables—which add diversity to the human diet and provide nutrients—are animal pollinated. Animal-pollinated crops, including several key oilseed species, also tend to be of greater economic value than are those not pollinated by animals, and they provide relatively higher income to growers. Moreover, bee pollination is required to produce the seeds of major forage and hay crops, such as alfalfa and clover, which are used to feed animals that, in turn, supply meat and dairy products. Thus, the contribution of pollinators to the quality of the human diet makes determining their status in North America an issue of prime importance.

Estimating the ecological value of pollinators and pollination and predicting the consequences of their losses are considerably more challenging than estimating their economic value in agriculture. Such estimates are complicated by both the number of species involved and the relative paucity of information available for most of these species (particularly those in natural communities). As discussed in Chapter 1, it is reasonable to assume that a large proportion of flora in uncultivated terrestrial communities of North America rely upon pollinators to some degree. In a recent assessment of the susceptibility of ecosystem services to species losses (Chapter 1), animal-mediated pollination is considered a service for most ecosystems and losses of pollinator would affect trophic stability.

Among the first topics examined was the question of how to differentiate between pollinator *shortage* and pollinator *decline*. Shortages and declines were recognized as distinct but not necessarily related phenomena. Shortages entail insufficient supply to meet demand according to recognized norms; declines are trends toward reduction in population size or diversity over time (Chapter 2). Using these definitions, the committee evaluated the literature and consulted numerous experts to try to determine the status of major groups of animal pollinators.

MANAGED POLLINATORS

Status

Population status of most managed pollinators, such as bumble bees and alfalfa leafcutting bees, are not closely monitored in North America. Evidence for decline is compelling for the honey bee (*Apis mellifera*), which is among the few actively managed pollinator species. Current methods for documenting the status of managed colonies of *A. mellifera*, a species of enormous economic importance (Chapter 1), are surprisingly inadequate

(Chapters 2 and 5). Although the U.S. Department of Agriculture's (USDA's) National Agricultural Statistics Service (NASS) tracks managed honey bee colonies, the surveys focus on honey production rather than on pollination. The result is the double-counting of some honey-producing colonies and the omission of others that do not produce honey for commercial sale in the United States (Chapter 2). Moreover, NASS data do not consider colony strength or quality. Because data are collected in the United States, Canada, and Mexico by different methods, making direct comparisons is difficult.

Recommendation: Improved information gathering for the beekeeping industry is critical, and the NASS should modify its data collection methodologies. The committee specifically recommends that NASS:

- Refine its assessment of honey bee abundance. The information would be more useful if all commercial honey bee colonies were counted annually and in one location only (as is currently done every 5 years for the census of agriculture). Greater accuracy also would be gained by determining whether colonies are leased for pollination, used to produce commercial honey, or both, and which use is primary. NASS should adjust its data collection to include the number of colonies lost during the previous year for any reason and the number lost over the previous winter. These data should be available by state to provide a broad picture of the overall health of the bee industry.
- Collect commercial honey bee pollination data from beekeepers and from crop growers. The availability of commercial honey bees as pollinators would be better understood if data were collected on the specific crops pollinated and on the leasing fees per colony by crop.
- Coordinate and reconcile data collection on honey bee colonies throughout North America. NASS should make its annual survey definitions compatible with its 5-year census of agriculture. The United States should work with Canada and Mexico through the North American Free Trade Agreement's Commission for Environmental Cooperation and the Trilateral Committee for Wildlife and Ecosystem Conservation and Management to adopt common methodologies.

Causes of Decline

Introduced parasites and diseases have contributed to declines in managed bees. Varroa mite has had a dramatic negative impact on the abundance of honey bees in North America. Bumble bees also have suffered from a number of parasites, notably the protozoan parasites *Nosema bombi* and *Crithidia bombi*, and the tracheal mite *Locustacris buchneri*. Chalkbrood,

a fungal disease caused by *Ascosphaera*, nearly destroyed the ability to produce alfalfa leafcutting bees in the United States.

For the first time since 1922, honey bees were imported in early 2005 from outside North America after a change in regulations promulgated under the terms of the Honeybee Act of 1922. Bee imports could increase the risk of introduction of pests and parasites.

Recommendation: The Animal and Plant Health Inspection Service (APHIS) should ensure that its regulations prohibit introduction of new pests and parasites along with imported bees, and Congress should expand the Honeybee Act of 1922 to include bomiculture and the fostering and breeding of other imported pollinator species. That is, Congress should extend in principle the Honeybee Act to other managed pollinator species.

Other factors also could contribute to current and potential future declines in honey bee populations: antibiotic-resistant pathogens (American foulbrood); pesticide use; and the encroachment of Africanized honey bees, particularly in the southeastern United States—a major regional source of packages, queens, and migratory beekeepers for the rest of the country.

Recommendation: Through research at the Agricultural Research Board (ARS) and competitive grant programs, USDA should not only continue, but also expand its efforts to:

- Encourage innovative approaches to protecting honey bee health by
 - developing sustainable management programs for varroa mites, including methods for managing pesticide resistance in mite populations;
 - identifying additional natural and synthetic pesticides and least-toxic alternatives for mite control and bee management (for example, pheromones); and
 - developing nonchemical cultural bee management practices.
- Improve genetic stocks of honey bees by
 - refining methods for identifying stocks with desirable traits and for breeding, selecting, maintaining, and improving stocks with such desirable traits as disease and pest resistance, moderated temperament, and improved honey production, taking advantage of the opportunities afforded by the recently sequenced honey bee genome;
 - refining methods for high-quality queen production from selected stocks including controlling mating (for example

- instrumental insemination, isolated mating, and drone saturation) to ensure expression of desired traits in colonies;
- expanding current efforts in germplasm preservation, including cryopreservation;
 - developing methods for the maintenance of European stocks in areas of Africanization;
 - developing a third-party certification program to ensure the quality and effectiveness of commercial queens marketed or advertised as being parasite- or pathogen-resistant (or any other specific trait); and
 - identifying markers (expressed sequence tags and quantitative trait loci) as a support to breeding programs (Chapter 6).

The achievement of these objectives will be possible only if ARS maintains current support for research and restores lost positions for scientists. A special focus will need to be placed on honey bee pollination, and reward systems for technology transfer should be developed within ARS. Although honey bees are important pollinators, there also are commercially important non-*Apis* species that require attention. The development of management protocols for wild species and the management of agricultural landscapes to better sustain wild pollinator populations can help supplement honey bee populations and reduce the risks associated with sole reliance on a single pollinator, particularly as pollinator demands rise and shortages become likely.

Recommendation: The USDA ARS should:

- Create research entomology positions in its fruit and vegetable laboratories in geographically diverse regions of the United States to work on developing new non-*Apis* pollinators for major crops, on identifying those with potential for use as commercial pollinators, and on establishing protocols for management. These activities should augment work in the Bee Biology and Systematics Laboratory in Logan, Utah, which currently serves as a focal point for non-*Apis* research.
- Develop and implement bombiculture disease management programs to prevent pathogen spillover to wild populations.
- Address pathogen problems in culturing alfalfa leafcutting bees (megachileculture) to improve population sustainability and crop pollination efficacy.
- Conduct and encourage research on landscape and farm management as related to pollinator populations and communities, and ARS should provide guidance on pollinator-friendly management practices.

Recommendation: Private-sector funding mechanisms for honey bee health and technology transfer from federal, state, and university research facilities should be created and enhanced to meet pollination needs. Industry check-off programs, which now cover crop commodities and honey, could add honey bee pollination services to the scope of existing programs. Check off programs collect funds from an agricultural commodity group to support research and promote the commodity. This private-sector effort could complement federally funded basic research efforts and promote translational research.¹

Consequences of Decline

Pollinator declines will not jeopardize food supplies because grains—the world’s primary sources of dietary energy—do not depend upon animal pollinators. However, supplies of animal-pollinated foods—fruits, vegetables, and some nuts—would be affected. Among the most conspicuous demonstrable consequences of changing pollinator status in agriculture are the rising costs of pest control in apiculture (and hence rising costs for honey bee rental) that accrue from the mite management required to maintain stable honey bee populations. Honey bee rental costs also are rising because of an increase in demand from almond growers that resulted from acreage increases and seasonal instability in honey bee populations. Despite overwhelming reliance on one species, few alternative actively managed species are being used. And despite evidence of their efficacy as crop pollinators, wild species are not being exploited to the extent possible.

Recommendation: USDA should establish discovery surveys for crop pollinators throughout the range of crops in North America to identify the contributions of wild species to agricultural pollination.

WILD POLLINATORS

Status

The committee found that the strength of the evidence for population status varies from one taxon to another. In parts of their ranges, the declines in several vertebrate pollinator species, particularly bats, are evidenced by conservation program monitoring. Long-term studies by individual investigators and regional Heritage Programs also provide evidence for declines (and possible extinction in some cases) among bumble bee species and some

¹Translational research is the process of applying ideas, insights, and discoveries generated through basic scientific inquiry to industrial or agricultural uses.

butterflies as do recent additions to endangered species lists (Chapter 2). Many other pollinators (including several flies, wasps, and beetles) could be declining, even rapidly, but insufficient data are available to provide unambiguous documentation of trends. Historical data could be collected by mining museum collections. However, data mining could be difficult for species that are not well described. Insects that constitute the majority of pollinator species are less well described—taxonomically or ecologically—than are other animal pollinators. In fact, taxonomic impediments for insects are enormous with respect to documenting declines (Chapter 2).

Recommendation: To address the taxonomic impediment to assessing pollinator status, the USDA's ARS should expand basic research on the systematics of pollinators and on the development of rapid identification tools.

Causes of Decline

The causes of decline or factors contributing to it could be assigned definitively in only a few cases (Chapter 3). Decline in populations of some native bumble bees appears to be the result of infection with non-native protozoan parasites, including *Nosema bombi* and *Crithidia bombi*. These parasites probably came from commercial bumble bees imported from Europe for greenhouse pollination. The managed bees used in greenhouse pollination often harbor high pathogen loads, and when they escape from greenhouses, pathogen spillover into native species occurs. For some species, competition with exotic pollinators (including honey bees) can lead to population declines. Declines in many pollinator taxa also are thought to be associated with habitat loss, fragmentation, and deterioration, although in North America, data are in most cases inadequate to demonstrate causation unambiguously. One exception is the decline in bat populations that is associated with destruction of cave roosts, but there is evidence that other factors also contribute to pollinator species decline. Changes in the phenology of interactions, ranges, and distributions that lead to loss of synchrony (possibly because of global climate change) and to disruption of migratory routes (making migration an endangered phenomenon) are posited for hummingbirds, nectar-feeding bats, and some butterflies and moths.

Recommendation: To prevent pathogen spillover to wild populations, APHIS should require that any commercially produced bumble bee colony shipped within the United States be certified as disease free.

Consequences of Decline

The consequences of pollinator decline in nonagricultural systems are more difficult to document. Few plant species rely on a single pollinator; many have more than one. Nevertheless, there are documented examples of reduced fruit and seed set in native plants apparently in response to a paucity of pollinators. Pollen limitation of seed set is common in wild plants, but its population consequences are not clear. In the event of declining pollinator populations, some plant populations could become more vulnerable to an extinction vortex—the interacting factors that serve to progressively reduce small populations—because of the increased risks of incurring the demographic and genetic consequences of small population size. These include genetic erosion, inbreeding depression, decreased reproductive success, and greater susceptibility to catastrophes and random changes in environmental conditions. Therefore, the effects of pollinator decline on rare plant species or on those with small populations also should be given special attention.

Recommendation: The U.S. Geological Survey, the Fish and Wildlife Service, and other agencies responsible for natural resource protection should establish discovery surveys for pollinators of rare, threatened, and endangered plant species.

Monitoring

Little is known about the status of most wild pollinators in North America because there is seldom a historical baseline with which modern data can be compared. The committee notes that systematic, thorough monitoring programs in Europe have revealed dramatic declines in pollinator abundance and diversity (Chapter 5); there are no comparable North American programs. The European experience demonstrates that monitoring is needed to document changes in populations and diversity, and that monitoring programs profit from contributions by citizen-scientists. The quality and validity of the information obtained by citizen-scientists' monitoring should be tested and calibrated against professional science monitoring.

Two sampling strategies could compensate for the absence of baseline data. First, existing historical data could be used in conjunction with contemporary survey data to guide focused assessments of the status of pollinators in specific regions of North America. Second, a long-term annual monitoring program could be initiated expressly to establish baseline data for comparison at different times in the future. In contrast to an assessment that provides a one-time snapshot, such monitoring can elucidate trends in species abundance and in the relationships between changes in community composition and their putative environmental causes. Understanding those

relationships is crucial for developing plans to mitigate environmental change and to manage for species persistence.

Recommendation: The federal government should establish a network of long-term pollinator-monitoring projects that use standardized protocols and joint data-gathering interpretation in collaboration with Canada and Mexico. A rapid, one-time assessment of the current status of wild pollinators in North America to establish a baseline for long-term monitoring is a laudable initial goal.

Components of this two-part assessment and monitoring program should include:

- assessment that targets re-surveys of areas that had been well sampled in the past and mining museum collections (specimens and labels) and the literature for historical data that correspond to areas of continuous, high-intensity sampling;
- monitoring that integrates the work of professional scientists and citizen-scientists in tracking pollinator status and pollination function to maximize the depth and breadth of effort.

The selection of study species should correspond to the strength of evidence for decline. In view of collective evidence of population declines, bees would provide a logical initial focus. Lepidoptera constitute another group for which a compelling need for monitoring exists, given recent extinctions and the classifications of some species as endangered or threatened.

Conservation and Restoration

Conservation and restoration are crucial to the preservation of pollinator populations and diversity, but more must be learned about pollinator biology. Research on the basic biology and ecology of wild pollinators is inadequate.

Recommendation: Because of the importance of pollination as an ecosystem service in both agricultural and natural ecosystems, the National Science Foundation and USDA should recognize pollination as a cross-cutting theme in their competitive grant programs and work together to integrate research that ranges from the genomics of honey bees and the systematics and ecology of wild pollinators to the effects of global climate change on pollinator-plant interactions. Representative areas where research is needed include:

- Multidisciplinary research that promotes sustainable pollinator populations;
- Identification of causes and consequences (genetic erosion and pollen limitation) of pollinator decline;
- Ecology, restoration, conservation, and management of pollinators and pollination services, including investigation of effects of invasive plants and animals on pollination systems; and
- Small Business Innovation Research programs to promote technology transfer to address the health and sustainability of commercially managed pollinators.

Despite sketchy data on wild pollinators, there are viable pollinator-friendly land management practices. These include, for example, providing corridors to link habitat fragments and thus to encourage pollinator movement; configuring landscape fragments to maintain pollinator populations, communities, and functions; using low- and no-till agriculture to preserve native pollinators' nests in fields; and setting aside land for field margins to provide nesting habitat and forage for pollinators. However, these practices are not in wide use (Chapter 6), and land managers should be offered economic incentives to adopt such practices.

Recommendation: Economic incentives should be expanded for pollinator conservation.

- State-level Natural Resources Conservation Service (NRCS) offices should provide lists of scientifically tested and approved pollinator-friendly practices to farmers participating in USDA cost-share programs (the Wildlife Habitat Incentives Program and the Environmental Quality Incentives Program), land retirement programs (the Conservation Reserve Program [CRP] and the Conservation Reserve Enhancement Program), and the production stewardship programs (Conservation Security Program [CSP]).
- CRP should explicitly incorporate pollinator habitat in the environmental-benefits index used to evaluate land parcel proposals.
- CSP should incorporate the value of pollinator habitat development into its determination of the stewardship tiers that are the basis for federal payments.
- USDA cost-sharing, land retirement, and production stewardship programs should be available to producers of all commodities—fruits, nuts, and vegetables—that depend on pollinators.
- The NRCS should target new hiring of personnel whose expertise is in biological sciences, especially ecology and natural-area management.

As discussed in Chapter 5, a two-part program to assess the current

status of wild pollinators in North America and to establish a framework for long-term monitoring of pollinator populations and function over time is a laudable goal. New long-term monitoring programs should maximize results obtained per dollar spent by integrating professional scientist monitoring activity with citizen-scientist monitoring activity in assessing both pollinator status and pollination function. The professional science activities fall within the mandate of governmental agencies, including the USDA, the U.S. Geological Survey, the U.S. Fish and Wildlife Service, and the National Science Foundation's proposed National Ecological Observatory Network. The citizen-scientist activities could be coordinated through partnerships among nongovernmental organizations (NGOs), governmental organizations, and citizen groups. Participating NGOs for a North American Pollination Monitoring Program could include the North American Pollinator Protection Campaign, the Xerces Society, Monarch Watch, and likely citizen-scientist groups such as native plant societies, gardening clubs, schools, friends of nature reserves, community farm alliances, or commodity groups. The Pollinator Watch Program in Canada is currently under development through the Environmental Monitoring and Assessment Network's Nature Watch Program (<http://www.eman-rese.ca/eman/naturewatch.html>). Federal agencies could stimulate collaborative programs that encourage agency, university, and NGO scientists to work together via strategically formulated funding announcements. The participation of volunteer citizen-scientists through the NGOs could greatly increase the output of assessment programs at little additional cost.

Nonfarm landowners, such as homeowners and private businesses, also could contribute to conservation of pollinators, with little investment (Box 6-3). Wildflower plantings provide resources for bees, and wood fences can provide nesting sites for twig-nesting bees. Raising public awareness and educating the next generation about the importance of pollinators and what people could do to protect them is critical.

Recommendation: As part of their outreach, federal granting agencies should make an effort to enhance public understanding of the importance of pollination as an ecosystem service through support for citizen-scientist monitoring programs, teacher education, and K-12 and general public education efforts that center on pollination.

Recommendation: Professional societies (Ecological Society of America, Entomological Society of America, American Association of Professional Apiculturists, Botanical Society of America) and NGOs (North American Pollinator Protection Campaign, Xerces Society for the Preservation of Endangered Invertebrates) should collaborate with landowners and the public to increase awareness of the importance of pollinators and to pub-

licize simple activities the public can do to promote and sustain pollinator abundance and diversity.

Although the object of the Endangered Species Act of 1973 (ESA) is to protect endangered species and their habitats, many endangered pollinators are not recognized candidates for endangered or threatened status. Congress directed that listing of a species required a scientific determination of its continued existence as threatened or endangered, but data on many pollinators are sparse. Also, a 1981 congressional revision of the ESA specifically exempted any “species of the Class Insecta determined by the Secretary to constitute a pest whose protection under the provisions of this Act would present an overwhelming and overriding risk to man.” Some caterpillars and carpenter bees, for example, can cause or have the potential to cause damage, so it could be difficult to use ESA to achieve protection for those species.

Recommendation: Congress should not consider any ESA amendment that would create additional barriers to listing pollinator species as endangered.

Glossary

Africanized honey bee	<i>Apis mellifera scutellata</i> , originally from central and south Africa, taken to Brazil in 1957, migrated northward through South and Central America, finally to the southern regions of the United States. Noted for defending nests vigorously and for throwing off swarms any time of the year.
Allee effect	Inverse density dependence at low densities. For example, seed set can decline drastically at low plant densities if pollinators cannot find plants to effect cross-pollination.
American foul brood	A bacterial disease (caused by <i>Paenibacillus</i>) of honey bees that produces a foul odor in dead bee larvae. A similar disease is called European foul brood.
Anther	Pollen-bearing portion of a stamen.
Apiary	Groups of hives that contain honey bee colonies; apiaries are sometimes called outyards.
Autogamy	The quality of self-fertility and self-pollinating in plants.
Bee hive	The physical construct for honey bees: a hollow tree, a Langstroth hive, a woven straw skep, or any other container of the right volume and physical properties.
Beeswax	A complex lipoidal secretion from the four-paired wax glands of young worker bees.

Bombiculture	Domestication of bumble bees for commercial propagation.
Brood	The eggs, larvae, and pupae within a honey bee or bumble bee colony. Immature honey bees live in the central portion of older darkened combs; pollen and honey are stored at the periphery of the brood area.
Bulbil	Asexual bulb-shaped reproductive unit of agaves and other plants. Bulbils are produced on flowering stalks if pollinators fail to visit flowers; they are not produced by fertilization. Seeds are not produced and before the death of the semelparous plant, clonal, tiny agaves grow from the unfertilized flowers.
Bumble bee	Bee of the genus <i>Bombus</i> , widely distributed throughout North America and some other continents. Bumble bees are social and have annual colonies; some species are managed commercially for greenhouse pollination, especially of tomatoes.
Buzz pollination	The process by which a pollinator—usually bumble bee or a solitary bee, but not a honey bee—attaches itself to a flower and vibrates its flight muscles. The pollinator's movement causes pollen to be dislodged from the anther.
Carpenter bee	Large solitary bee that lays eggs in tunnels bored into wood or plant stems.
Colony	Social insects including honey bees organized by caste (sterile female workers, male drones, a queen mother). The bee colony has been labeled a superorganism, and it can have as many as 60,000 individuals at its peak. The colony lives in a hive or nest. Bumble bee colonies are annual and much smaller (fewer than 30 bees at high altitudes) than are honey bee colonies.

<i>Crithidia bombi</i>	An intestinal parasite (trypanosome) of bumble bees.
Cross-pollination	Pollination by pollen from another plant.
Dioecia	The condition of plants with staminate and pistillate flowers borne on separate individuals.
Drone	A male honey bee that does not forage for itself at flowers, but is fed by its sisters. Haplodiploid genetic sex determination in bees, ants, and wasps results in males having one set of chromosomes. Drones are haploid; their sisters have two sets of chromosomes and are diploid. Drone bees develop from unfertilized eggs.
Event selection	Selection for successful genetic transformation of a plant (for example, corn) with a genetically engineered sequence.
Extinction vortex	Interaction of multiple factors that progressively forces an already small population into extinction.
Fecundity	Ability to reproduce regularly and easily; typically measured in plants as fruit set or seed set.
Floret	A small flower in the composite (Asteraceae) inflorescence or the spike of a grass.
Founder effect	Genetic drift that results from the founding of a population by a small number of individuals.
Fruit set	Formation of fruit as a result of pollination and fertilization.
Geitonogamy	Pollination by pollen from another flower on the same plant.
Genetic drift	Change in the gene pool of a small population attributable to chance (Campbell et al., 1999).

Haplodiploidy	Sex determination in bees, ants, and wasps. The queen controls whether eggs are fertilized. The females, which emerge from fertilized eggs, are workers and diploid with both sets of chromosomes. Males are haploid, coming from unfertilized eggs and having only one set of chromosomes.
Hemizyosity	The state of having unpaired genes in an otherwise diploid cell.
Hermaphrodite	An organism that has male and female reproductive organs, for example, plants with perfect flowers.
Heterozygosity	The state of possessing different alleles of the same gene.
Hive	The location (the tree, Langstroth hive box, or similar cavity) of a honey bee colony. Also called the nest or nest box.
Homozygosity	The state of possessing two identical alleles of the same gene.
Honey bee	A social, honey-making bee of the genus <i>Apis</i> , found mostly in tropical Asian regions.
Inbreeding	The breeding of closely related plants or animals; in plants, it occurs generally by repeated self-pollination (Raven et al., 2005).
Larva	Immature stage of insect species that undergo metamorphosis (caterpillar, grub, maggot).
Leafcutter bee	Bee in the family Megachilidae that cuts rounded pieces from leaves and flowers to line its nest.
Megachileculture	Culture of leafcutter bees for commercial propagation.

Migratory beekeepers	Beekeepers who take their hives from one place to another. They exploit ephemeral blooms to make specialty honey or to provide pollination service.
Monoecious	Staminate and pistillate flowers borne on the same plant.
Nectar	The sugary often complex watery mixture produced by secretory glands within flowers and from extrafloral nectaries. The high-energy sugar fuel sought by bees and other pollinators, which typically also contains amino acids. A floral reward exchanged for pollination services.
Nectar robbing	Extraction of nectar through a hole pierced in the corolla, a practice of some short-tongued bumble bees and carpenter bees that allows them to extract nectar from long-tubed flowers.
Nosema	A bee disease caused by a protozoan (<i>Nosema apis</i>). <i>Nosema bombi</i> is a disease of bumble bees.
Ovule	A structure in seed plants containing the female gametophyte with an egg cell; when fertilized and mature, an ovule becomes a seed.
Package bees	A 2–3-lb aggregation of bees supplied by a breeder. Packages are used to start new colonies.
Parthenocarpy	Fruit production in flowering plants without pollination. Parthenocarpy can be induced by plant hormones or genetic modification.
Perfect flower	A flower that contains both male and female reproductive parts.
Pistil	Female reproductive organ of a flower that consists of a stigma, style, and ovary.

Pollen	The male sex cells of flowering plants (angiosperms) that are found within the microscopic tough-shelled pollen grains. Pollen must be moved from flower to flower for fertilization. The sex cells travel down pollen tubes that grow through the floral style and fertilize the ovules. Seeds develop within the ovary and the fruit forms. Pollen grains also are the indispensable protein and lipid-rich food of bees and many other pollinators.
Pollination	The transfer of pollen grains from flower to flower and usually plant to plant by wind, water, or animals.
Queen bee	The mother of the bees in a nest; usually a single queen inhabits a mature bee colony. The queen can lay 1,500 or more eggs per day during her lifespan of 2–3 years. If a queen dies, the colony can produce a new queen from a diploid worker egg.
Seed set	Formation of seeds, typically after pollination.
Self-compatibility	The condition that allows a plant to accept fertilization by its own pollen.
Self-incompatibility	The condition that prevents a plant from accepting fertilization by its own pollen.
Self-pollination	Pollination by pollen from the same flower or same plant (see geitonogamy); selfing.
Split or divide	Beekeepers can divide or split half of the adults, brood, and honey combs from a populous mother colony into two Langstroth hive boxes. A new queen is supplied to the daughter colony, or the bees are allowed to be queenless for a time and to raise a new queen from an egg laid by the old queen.
Stamen	Male reproductive organ of a flower that typically includes a filament bearing an anther.

Stigma	Region of a carpel (female productive organ of a flower) that serves as a receptive surface for pollen grains and on which they germinate.
Tracheal mite	<i>Acarapis woodi</i> , parasite of honey bees, accidentally introduced into the United States that has caused colony mortality in many locations.
Trioecious	Staminate, pistillate, and perfect flowers borne on different plants.
Varroa mite	<i>Varroa jacobsoni</i> , a parasite, accidentally introduced from Asia that became established in the United States. It continues to cause heavy mortality of bee colonies in some regions. The mite feeds externally on bee larvae and pupae within the brood combs.
Worker	One of the thousands of sterile daughters of the queen. Worker ovaries usually are undeveloped. Workers typically work inside and then outside the nest as foragers, living for only 4–6 weeks during the spring and summer months. Bumble bee queens also produce workers, but many fewer than honey bees.
Xenogamy	Cross-pollination and cross-fertilization of plants.

References

- AAAS (American Association for the Advancement of Science). 1994. Benchmarks for Science Literacy. Available at <http://www.project2061.org/publications/bsl/online/bolintro.htm>. Accessed May 31, 2006.
- ABF (American Beekeeping Federation). 2005. Honey Bee Pollination Crisis: Shortage of Bees May Reduce Crop Production. Available at: <http://abfnet.org/?p=51>. Accessed May 15, 2006.
- Abu-Asab, M.S., P.M. Peterson, S.G. Shetler, and S.S. Orli. 2001. Earlier plant flowering in spring as a response to global warming in the Washington, DC, area. *Biodiversity Conservation* 10:597–612.
- Acciarri, N., F. Restaino, G. Vitelli, D. Perrone, M. Zottini, T. Pandolfini, A. Spena, and G.L. Rotino. 2002. Genetically modified parthenocarpic eggplants: improved fruit productivity under both greenhouse and open field cultivation. *BMC Biotechnology* 2:4.
- Adey, M., P. Walker, and P.T. Walker. 1986. *Pest Control Safe for Bees. A Manual and Directory for the Tropics and Subtropics*. Cardiff: International Bee Research Association. 224 pp.
- Adlerz, W.C. 1966. Honey bee visit numbers and watermelon pollination. *Journal of Economic Entomology* 59:28–30.
- Agosti, D., and N.F. Johnson, eds. 2005. *Antbase*. Available at: Antbase.org, version (May 2005).
- Agosti, D., J.D. Majer, L.E. Alonso, and T.R. Schultz, eds. 2000. *Ants: Standard Methods for Measuring and Monitoring Biodiversity*. *Biological Diversity Handbook Series*. Washington and London: Smithsonian Institution Press.
- Aizen, M.A., and P. Feinsinger. 1994. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology* 75:330–351.
- Alippi, A.M., G.N. Albo, D. Leniz, I. Rivera, M.L. Zanelli, and A.E. Roca. 1999. Comparative study of tylosin, erythromycin and oxytetracycline to control American foulbrood of honey bees. *Journal of Apicultural Research* 38(3–4):149–158.
- Allen, M.F., and B.V. Ball. 1996. The incidence and world distribution of the honey bee viruses. *Bee World* 77:141–162.

- Allen-Wardell, G., P. Bernhardt, R. Bitner, A. Burquez, S. Buchmann, J. Cane, P.A. Cox, V. Dalton, P. Feinsinger, M. Ingram, D. Inouye, C.E. Jones, K. Kennedy, P. Kevan, H. Koopowitz, R. Medellin, S. Medellin-Morales, and G.P. Nabhan. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology* 12(1):8–17.
- Altieri, M.A., and C.I. Nicholls. 2004. *Biodiversity and Pest Management in Agroecosystems*. 2nd edition. New York: Haworth Press.
- Altizer, S., W.M. Hochachka, and A.A. Dhondt. 2004. Seasonal dynamics of mycoplasmal conjunctivitis in eastern North American house finches. *Journal of Animal Ecology* 73:309–322.
- Ananthakrishnan, T.N. 1993. The role of thrips in pollination. *Current Science (Bangalore)* 65(3):262–264.
- Anderson, D.L., and J.W.H. Trueman. 2000. *Varroa jacobsoni* (Acari: Varroidae) is more than one species. *Experimental and Applied Acarology* 24:165–189.
- Anderson, P.L., R.L. Hellmich, R. Jarrad, J.R. Prasifka, and L.C. Lewis. 2005. Effects on fitness and behavior of monarch butterfly larvae exposed to a combination of Cry1Ab-Expressing corn anthers and pollen. *Environmental Entomology* 34(4):944–952.
- Anderson, R.P., M. Gomez-Laverde, and A.T. Peterson. 2002. Geographical distributions of spiny pocket mice in South America: insights from predictive models. *Global Ecology and Biogeography* 11:131–141.
- Anonymous. 1987. *Varroa* mites found in the United States. *American Bee Journal* 127:745–746.
- Anonymous. 2005. Minnesota beekeepers and DNR settle claims. *Bee Culture* 133:51.
- Aratanakul, P., and M. Burgett. 1975. *Varroa jacobsoni*: a prospective pest of honeybees in many parts of the world. *Bee World* 56:119–121.
- Arita, H.T. 1993. Conservation biology of the cave bats of Mexico. *Journal of Mammalogy* 74:693–702.
- Arita, H.T., and K. Santos-del-Prado. 1999. Conservation biology of nectar-feeding bats in Mexico. *Journal of Mammalogy* 80:31–41.
- Arizaga, S., and E. Ezcurra. 1995. Insurance against reproductive failure in a semelparous plant—Bulbil formation in *Agave macroacantha* flowering stalks. *Oecologia* 101:329–334.
- Arizaga, S., and E. Ezcurra. 2002. Propagation mechanisms in *Agave macroacantha* (Agavaceae), a tropical arid-land succulent rosette. *American Journal of Botany* 89:632–641.
- Arizaga, S., E. Ezcurra, E. Peters, F.R. de Arellano, and E. Vega. 2002. Pollination ecology of *Agave macroacantha* (Agavaceae) in a Mexican tropical desert. I. Floral biology and pollination mechanisms. *American Journal of Botany* 87:1004–1010.
- Arizmendi, M.C., and J.F. Ornelas. 1990. Hummingbirds and their floral resources in a tropical dry forest in Mexico. *Biotropica* 22:172–180.
- Arizona Game and Fish Department. 2006. Heritage Data Management System. Available at: http://www.azgfd.gov/w_c/edits/documents/Leptcuye.fi.pdf. Accessed May 19, 2006.
- Armstrong, J.A. 1986. Floral biology of *Myristica fragrans* Houtt. (Myristicaceae), the nutmeg of commerce. *Biotropica* 18:32–38.
- Arroyo-Cabrales, J., R.R. Hollander, and J.K. Jones, Jr. 1987. *Choeronycteris mexicana*. *Mammalian Species* 291:1–5.
- Asai, W.K. 2005. Nuts: striving for higher yields. *American Fruit Grower* 125:90.
- Ascher, J.S. 2001. *Hylaeus hyalinatus* Smith, a European bee new to North America, with notes on other adventive bees (Hymenoptera: Apoidea). *Proceedings of the Entomological Society of Washington* 103:184–190.
- Asher, J., M. Warren, R. Fox, P. Harding, G. Jeffcoate, and S. Jeffcoate. 2001. *Millennium Atlas of Butterflies in Britain and Ireland*. Oxford: Oxford University Press.

- Ashman, T.L., T.M. Knight, J.A. Steets, P. Amarasekare, M. Burd, D.R. Campbell, M.R. Dudash, M.O. Johnston, S.J. Mazer, R.J. Mitchell, M.T. Morgan, and W.G. Wilson. 2004. Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology* 8:2408–2421.
- Asikainen, E., and P. Mutikainen. 2005. Preferences of pollinators and herbivores in gynodioecious *Geranium sylvaticum*. *Annals of Botany* 95(5):879–886.
- Asner, G.P., A.J. Elmore, L.P. Olander, R.E. Martin, and A.T. Harris. 2004. Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources* 29:261–299.
- Bailey, A.M., and R.J. Niedrach. 1965. *Birds of Colorado*. Denver: Denver Museum of Natural History. Vol. 1–2, 895 pp.
- Baker, H.G. 1975. Sugar concentrations in nectars from hummingbird flowers. *Biotropica* 7:37–41.
- Baker, H.G., and P.D. Hurd, Jr. 1968. Intrafloral ecology. *Annual Review of Entomology* 13:385–414.
- Baker, H.G., I. Baker, and S.A. Hodges. 1998. Sugar composition of nectars and fruits consumed by birds and bats in the tropics and subtropics. *Biotropica* 30:559–586.
- Baker, J.D.R., and W. Cruden. 1991. Thrips-mediated self-pollination of two facultatively xenogamous wetland species. *American Journal of Botany* 78:959–963.
- Baker, R.J., L.C. Bradley, R.D. Bradley, J.W. Dragoo, M.D. Engstrom, R.F. Hoffmann, C.A. Jones, F. Reid, D.W. Rice, and C. Jones. 2003. Revised Checklist of North American Mammals North of Mexico, 2003. Occasional Paper OP-229. Lubbock, Tex.: Museum of Texas Tech University, NSLR Publications. 24 pp.
- Banda, H.J., and R.J. Paxton. 1991. Pollination of greenhouse tomatoes by bees. *Acta Horticulturae* 288:194–198.
- Banks, R.C., and W.A. Calder. 1989. Did Lewis and Clark discover the broad-tailed hummingbird (*Selasphorus platycercus*). *Archives of Natural History* 16:243–244.
- Barg, R., S. Shabtai, N. Carmi, M. Pilowsky, and Y. Salts. 2001. Transgenic parthenocarpy in determinate and indeterminate tomato cultivars. *Acta Horticulturae* 560:207–210.
- Barkin, D. 2003. Alleviating poverty through ecotourism: promises and reality in the monarch butterfly reserve of Mexico. *Environment, Development and Sustainability* 5:371–382.
- Barrett, D.P. 1955. History of American foulbrood in Michigan: period 1927–1954. *Gleanings in Bee Culture* 83:460–461.
- Barth, F.G. 1985. *Insects and Flowers: The Biology of a Partnership*. Translated from German by M.A. Biederman-Thorson. Princeton University Press. 297 pp.
- Barth, F.G. 1991. *Insects and Flowers: The Biology of a Partnership*. Translated from German by M.A. Biederman-Thorson. Princeton University Press. 408 pp.
- Barthell, J.F., and R.W. Thorp. 1995. Nest usurpation among females of an introduced leaf-cutter bee, *Megachile apicalis*. *Southwestern Entomologist* 20:117–124.
- Barthell, J.F., G.W. Frankie, and R.W. Thorp. 1998. Invader effects in a community of cavity nesting megachilid bees (Hymenoptera: Megachilidae). *Environmental Entomology* 27:240–247.
- Barthell, J.F., J.M. Randall, R.W. Thorp, and A.M. Wenner. 2001. Promotion of seed set in yellow star-thistle by honey bees: evidence of an invasive mutualism. *Ecological Applications* 11(6):1870–1883.
- Bartholomew, C.S., and K.V. Yeargan. 2001. Phenology of milkweed (Asclepiadaceae) growth and monarch (Lepidoptera: Nymphalidae) reproduction in Kentucky and ovipositional preference between common and honeyvine milkweed. *Journal of the Kansas Entomological Society* 74:211–220.
- Batabyal, A.A., and P. Nijkamp. 2005. Alternate strategies for managing resistance to antibiotics and pesticides. *Environmental Economics and Policy Studies* 7(1):39–51.

- Batra, S.W.T. 1979. *Osmia cornifrons* and *Pithitis smaragdula*, two Asian bees introduced into the United States for crop pollination. Proceedings of the Fourth International Symposium on Pollination, Maryland Agriculture Experiment Station Special Publication 1: 307–312.
- Batra, S.W.T. 1982. The hornfaced bee for efficient pollination of small farm orchards. Research for small farms. Pp. 116–120 in Research for Small Farm, USDA Miscellaneous Publication 1422, W.H. Kerr and L.V. Knutson, eds.
- Batra, S.W.T. 1994a. *Anthophora plumipes villosula* Sm. (Hymenoptera: Anthophoridae), a manageable Japanese bee that visits blueberries and apples during cool, rainy, spring weather. Proceedings of the Entomological Society of Washington 96:98–119.
- Batra, S.W.T. 1994b. Diversify with pollen bees. American Bee Journal 134:591–593.
- Batra, S.W.T. 1998. Hornfaced bees for apple pollination. American Bee Journal 138(5):361–365.
- Batra, S.W.T. 2003. Bee introductions to pollinate our crops. Pp. 85–98 in For Nonnative Crops, Whence Pollinators of the Future? K. Strickler and J.H. Cane, eds. Proceedings, Entomological Society of America. Lanham, Md.: Thomas Say Publications in Entomology.
- Bawa, K.S. 1974. Breeding systems of tree species of a lowland tropical community. Evolution 28:85–92.
- Bawa, K.S. 1990. Plant-pollinator interactions in tropical rain forests. Annual Review of Ecology and Systematics 21:399–422.
- Baxter, J., F. Eischen, J. Pettis, W.T. Wilson, and H. Shimanuki. 1998. Detection of fluvalinate-resistant varroa mites in U.S. honey bees. American Bee Journal 138:291.
- Baxter, J.R., M.D. Ellis, and W.T. Wilson. 2000. Field evaluation of ApistanReg and five candidate compounds for parasitic mite control in honey bees. American Bee Journal 140(11):898–900.
- Beattie, A.J. 1985. The Evolutionary Ecology of Ant-Plant Mutualisms. New York: Cambridge University Press.
- Bednarek, A.T., and D.D. Hart. 2005. Modifying dam operations to restore rivers: ecological responses to Tennessee river dam mitigation. Ecological Applications 15:997–1008.
- Beetsma, J. 1994. The varroa mite, a devastating parasite of western honeybees and an economic threat to beekeeping. Outlook on Agriculture 23:69–175.
- Belzunces, L.P., C. Pelissier, and G.B. Lewis, eds. 2001. Hazards of Pesticides to Bees. Paris: INRA Editions.
- Benting, J., I. Hauser-Hahn, R. Nauen, and R. Beffa. 2004. Molecular diagnosis of resistance. Pflanzenschutz-Nachrichten-Bayer 57(1):78–86.
- Berenbaum, M.R. 2001. Interpreting the scientific literature: differences in the scientific and lay communities. Plant Physiology 125:509–512.
- Berger, J. 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions. Conservation Biology 4:91–98.
- Bergström, G., P. Bergman, M. Appelgren, and J.O. Schmidt. 1996. Labial gland chemistry of three species of bumblebees (Hymenoptera: Apidae) from North America. Biorganic and Molecular Chemistry 4:515–519.
- Bernays, E.A., and M. Graham. 1988. On the evolution of host specificity in phytophagous arthropods. Ecology 69:886–892.
- Bernhardt, P. 1984. Mistletoes on mistletoes: the floral ecology of *Amyema miraculosum* and its host, *Amyema miquelii* (Loranthaceae). Australian Journal of Botany 28:437–451.
- Bernhardt, P. 1999. The Rose's Kiss; A Natural History of Flowers. Washington: Island Press/Shearwater Books.
- Bernhardt, P. 2000. Convergent evolution and adaptive radiation of beetle-pollinated angiosperms. Plant Systematics and Evolution 222:293–320.
- Bernhardt, P. and R. Edens. 2004. A fertility clinic for flora. Plant Talk 30:25–28.

- Bernhardt, P., and L.B. Thien. 1987. Self-isolation and insect pollination in the primitive angiosperms: new evaluations of older hypotheses. *Plant Systematics and Evolution* 156:159–176.
- Bertin, R.I. 1982. The ruby-throated hummingbird and its major food plants: ranges, flowering phenology, and migration. *Canadian Journal of Zoology* 60:210–219.
- Beye, M., M. Hasselmann, K. Fondrk, R.E. Page, Jr., and S.W. Omholt. 2003. The gene *csd* is the primary signal for sexual development in the honey bee and encodes a new SR-type protein. *Cell* 114:419–429.
- Bhattacharjee, Y. 2005. Ornithology—Citizen scientists supplement work of Cornell researchers—A half-century of interaction with bird watchers has evolved into a robust and growing collaboration between volunteers and a leading ornithology lab. *Science* 308:1402–1403.
- Biesmeijer J.C., S.P. Roberts, M. Reemer, R. Ohlemueller, M. Edwards, T. Peeters, A. Schaffers, S.G. Potts, R. Kleukers, C.D. Thomas, J. Settele, and W.E. Kunin. 2006. Parallel declines in pollinators and insect-pollinated plants in northwest Europe. Britain and the Netherlands. *Science* 313(5785):351–354.
- Bigger, D.S. 1999. Consequences of patch size and isolation for a rare plant: pollen limitation and seed predation. *Natural Areas Journal* 19:239–244.
- Blackburn, H.D. 2002. Management of U.S. genetic resources. Proceedings of the 7th World Congress on Genetics Applied to Livestock Production, Montpellier, France, August, 2002 Session 26, pp. 1–4. Montpellier: Institut National de la Recherche Agronomique (INRA).
- Bloch, D., N. Werdenberg, and A. Erhardt. 2006. Pollination crisis in the butterfly pollinated, wild carnation *Dianthus carthusianorum*? *New Phytologist* 169:699–706.
- Boecking, O., K. Bienefeld, and W. Drescher. 2000. Heritability of the varroa-specific hygienic behaviour in honey bees (Hymenoptera: Apidae). *Journal of Animal Breeding and Genetics* 117(6):417–424.
- Boggs, C.L., J.T. Smiley, and L.E. Gilbert. 1981. Patterns of pollen exploitation by Heliconius butterflies. *Oecologia* 48:284–289.
- Bogler, D.J., J.L. Neff, and B.B. Simpson. 1995. Multiple origins of the yucca-yucca moth association. *Proceedings of the National Academy of Sciences USA* 92:6864–6867.
- Bohart, G.E. 1958. Transfer and establishment of the alkali bee. In 10th Alfalfa Improvement Conference, Ithaca, NY, July 28–30, 4 pp.
- Bohart, G.E. 1962. How to manage the leaf-cutting bee for alfalfa pollination. Utah Agriculture Experimentation Station Circular 144, 7 pp.
- Bohart, G.E. 1967. Management of wild bees. Pp. 109–118 in *Beekeeping in the United States*, Agriculture Handbook. 335. Washington: U.S. Department of Agriculture.
- Bohart, G.E. 1970. Commercial production and management of wild bees—A new entomological industry. *Bulletin of the Entomological Society of America* 16(1):8–9.
- Bohart, G.E. 1972a. Management of wild bees for the pollination of crops. *Annual Review of Entomology* 17:287–312.
- Bohart, G.E. 1972b. Management of habitats for wild bees. Pp. 253–266 in *Proceedings Tall Timbers Conference on Ecological Animal Control by Habitat Management No. 3*.
- Bohart, G.E., and M.W. Pedersen. 1963. The alfalfa leaf-cutting bee, *Megachile rotundata* (F.), for pollination of alfalfa [lucerne] in cages. *Crop-Science* 3(2):183–184.
- Bond, W.J. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences* 344:83–90.
- Bond, W.J. 1995. Assessing the risk of plant extinction due to pollinator and disperser failure. Pp. 131–140 in *Extinction Rates*, J.G. Lawton and R.M. May, eds. Oxford University Press.

- Borror, D., C.A. Triplehorn, and N.G. Johnson. 1989. *An Introduction to the Study of Insects*. Philadelphia: Saunders College Publishing.
- Bosch, J., and W.P. Kemp. 1999. Exceptional cherry production in an orchard pollinated with blue orchard bees. *Bee World* 80(4):163–173.
- Bosch, J., and W.P. Kemp. 2000. Development and emergence of the orchard pollinator *Osmia lignaria* (Hymenoptera: Megachilidae). *Environmental Entomology* 29:8–13.
- Bosch, J., and W.P. Kemp. 2001. How to Manage the Blue Orchard Bee as an Orchard Pollinator. Sustainable Agriculture Network Handbook Series Book 5, National Agricultural Library, Beltsville, Md. 88 pp.
- Bosch, J., and W.P. Kemp. 2002. Developing and establishing bee species as crop pollinators: the example of *Osmia* spp. (Hymenoptera: Megachilidae) and fruit trees. *Bulletin of Entomological Research* 92(1):3–16.
- Bosch, J., W.P. Kemp, and S.S. Peterson. 2000. Management of *Osmia lignaria* (Hymenoptera: Megachilidae) populations for almond pollination: methods to advance bee emergence. *Environmental Entomology* 29(5):874–883.
- Boucher, D.H., ed. 1985. *The Biology of Mutualism: Ecology and Evolution*. New York: Oxford University Press.
- Bowlin, W.R., V.J. Tepedino, and T.L. Griswold. 1993. The reproductive biology of *Eriogonum pelinophilum* (Polygonaceae). Pp. 296–300 in *Proceedings of the Southwestern Rare and Endangered Plant Conference*, R. Sivinski and K. Lighffoot, eds. New Mexico State Forestry and Resources Conservation Division, Miscellaneous Publication #2.
- Brantjes, N.B.M. 1981. Ant, bee and fly pollination in *Epipactis palustris* (L.) Crantz (Orchidaceae). *Acta Botanica Neerlandica* 30:59–68.
- Brittain, W.H. 1933. Apple pollination studies in the Annapolis Valley, N.S., Canada 1928–1932. Canada Department of Agriculture Bulletin 162. 198 pp.
- Brody, A.K., and R.J. Mitchell. 1997. Effects of experimental manipulation of inflorescence size on pollination and pre-dispersal seed predation in the hummingbird-pollinated plant *Ipomopsis aggregata*. *Oecologia* 110:86–93.
- Bromenshenk, J.J., G.C. Smith, and V.J. Watson. 1995. Assessing ecological risks in terrestrial systems with honey bees. Pp. 9–30 in *Biomonitoring and Biomarkers as Indicators of Environmental Change*, F.M. Butterworth, ed. New York: Plenum Press.
- Bromenshenk, J.J., C.B. Henderson, R.A. Seccomb, S.D. Rice, R.T. Etter, S.F.A. Bender, P.J. Rodacy, J.A. Shaw, N.L. Seldomridge, L.H. Spangler, and J.J. Wilson. 2003. Can honey bees assist in area reduction and landmine detection? *Journal of Mine Action (Research, Development and Technology in Mine Action)*, Issue 7.3.
- Bronstein, J.L. 1988. Mutualism, antagonism and the fig-pollinator interaction. *Ecology* 69:1298–1302.
- Bronstein, J.L. 1994a. Our current understanding of mutualism. *Quarterly Review of Biology* 69:31–51.
- Bronstein, J.L. 1994b. Conditional outcomes in mutualistic interactions. *Trends in Ecology and Evolution* 9:214–217.
- Bronstein, J.L. 1995. The plant-pollinator landscape. Pp. 256–288 in *Mosaic Landscape and Ecological Processes*, L. Hansson, L. Fahrig, and G. Merriam, eds. London: Chapman and Hall.
- Bronstein, J.L., and D. McKey. 1989. The fig/pollinator mutualism: a model system for comparative biology. *Experientia* 45:601–604.
- Brown, D.G., K.M. Johnson, T.R. Loveland, and D.M. Theobald. 2005. Rural land-use trends in the conterminous United States, 1950–2000. *Ecological Applications* 15:1851–1863.
- Brown, K.S., and A.V.L. Freitas. 2000. Atlantic forest butterflies: indicators for landscape conservation. *Biotropica* 32(4B SI):934–956.
- Brown, M.J.F., R. Loosli, and P. Schmid-Hempel. 2003. Condition-dependent expression of virulence in a trypanosome infecting bumblebees. *Oikos* 91:421–427.

- Bruneau, A. 1997. Evolution and homology of bird pollination syndromes in *Erythrina* (Leguminosae). *American Journal of Botany* 84:54–71.
- Brys, R., H. Jacquemyn, P. Endels, F. Van Rossum, M. Hermy, L. Triest, L. De Bruyn, and G.D.E. Blust. 2004. Reduced reproductive success in small populations of the self-incompatible *Primula vulgaris*. *Journal of Ecology* 92:5–14.
- Bubalo, D., H. Pechhacker, E. Licek, N. Kezic, and D. Sulimanovic. 2005. The effect of *Varroa destructor* infestation on flight activity and mating efficiency of drones (*Apis mellifera* L.). *Wiener Tierärztliche Monatsschrift* 92:11–15.
- Buchmann, S.L. 1983. Buzz pollination in angiosperms. Pp. 73–114 in *Handbook of Experimental Pollination Biology*, C.E. Jones and R.J. Little, eds. New York: Scientific and Academic Editions.
- Buchmann, S.L. 1987. The ecology of oil flowers and their bees. *Annual Review of Ecology and Systematics* 18:343–369.
- Buchmann, S.L. 1996. Competition between honey bees and native bees in the Sonoran Desert and global bee conservation issues. Pp. 125–142 in *The Conservation of Bees*, A. Matheson, S.L. Buchmann, C. O’Toole, P. Westrich, and I.H. Williams, eds. New York: Academic Press.
- Buchmann, S.L., and J.S. Ascher. 2005. The plight of pollinating bees. *Bee World* 86:71–74.
- Buchmann, S.L., and G.P. Nabham. 1996. *The Forgotten Pollinators*. Washington: Island Press.
- Bugg, R.L., Anderson, J. H., Thomsen, C. D., and J. Chandler. 1998. Pp. 339–374 in *Enhancing Biological Control: Habitat Management to Promote Natural Enemies of Agricultural Pests*, R.L. Bugg, ed. Berkeley: University of California Press.
- Bull, J.J. 1983. *Evolution of Sex Determining Mechanisms*. Menlo Park: Benjamin Cummings Publishing Company.
- Burd, M. 1994. Bateman’s principle and plant reproduction: the role of pollen limitation in fruit and seed set. *Botanical Review* 60:83–139.
- Burgett, M. 1994. Pacific Northwest winter loss—1993/94. *National Honey Market News* 9:13–14. U.S. Department of Agriculture, Agricultural Marketing Service.
- Burgett, M. 2004. Pacific Northwest Honey Bee Pollination Survey—2003. *National Honey Report XXIII—1* (February 12, 2004):12–15. U.S. Department of Agriculture, Agricultural Marketing Service. Available at: <http://marketnews.usda.gov/portal/usda/templates/honey/honey2004/20040213hny.pdf>. Accessed December 28, 2005.
- Burgett, M. 2005. Pacific Northwest Honey Bee Pollination Survey—2004. *National Honey Report XXIV—1* (February 10, 2005):9–12. U.S. Department of Agriculture, Agricultural Marketing Service. Available at: <http://marketnews.usda.gov/portal/usda/templates/honey/honey2005/20050210hny.pdf>. Accessed December 15, 2005.
- Burgett, M., R.R. Rucker, and W.N. Thurman. 2004. Economics and honeybee pollination markets. *American Bee Journal* April 269–271.
- Búrquez, A. 2003. Flora and vegetation of the Gran Desierto and Rio Colorado of Northwestern Mexico. *Plant Systematics and Evolution* 231:11–7123.
- Búrquez, A., and A. Martínez-Yrizar. 1997. Conservation and Landscape Transformation in Sonora, México. *Journal of the Southwest* 39(3–4):371–398.
- Butaye, J., D. Adriaens, and O. Honnay. 2005. Conservation and restoration of calcareous grasslands: a concise review of the effects of fragmentation and management on plant species. *Biotechnology, Agronomy, Society and Environment* 9(2):111–118.
- Butler, G.D., and M.J. Wargo. 1963. Biological notes on *Megachile concinna* Smith in Arizona. *Pan-Pacific Entomologist* 39:201–206.
- Butz-Huryn, V.M.B. 1997. Ecological impacts of introduced honeybees. *Quarterly Review of Biology* 72:275–297.
- Caldas, A., and R.K. Robbins. 2003. Modified Pollard transects for assessing tropical butterfly abundance and diversity. *Biological Conservation* 110:211–219.

- Calder, W.A. 1987. Southbound through Colorado—Migration of rufous hummingbirds. *National Geographic Research* 3:40–51.
- Calder, W.A. 2004. Rufous and broad-tailed hummingbirds—Pollination, migration, and population biology. Pp. 59–79 in *Conserving Migratory Pollinators and Nectar Corridors in Western North America*, G.P. Nabhan, ed. Tucson: University of Arizona Press.
- Calder, W.A., and L.L. Calder. 1992. Broad-tailed hummingbird (*Selasphorus platycercus*). The Birds of North America, No. 16, A. Poole and F. Gill, eds. Philadelphia: The Academy of Natural Sciences; Washington: The American Ornithologists' Union.
- Calder, W.A., S.M. Hiebert, N.M. Waser, D.W. Inouye, and S.J. Miller. 1983. Site fidelity, longevity, and population dynamics of broad-tailed hummingbirds: a ten year study. *Oecologia* 56:689–700.
- Calderone, N.W. 2000. Effective fall treatment of *Varroa jacobsoni* (Acari: Varroidae) with a new formulation of formic acid in colonies of *Apis mellifera* (Hymenoptera: Apidae) in the northeastern United States. *Journal of Economic Entomology* 93:1065–1075.
- Calderone, N.W. 2005. Evaluation of drone brood removal for the management of *Varroa destructor* (Acari: Varroidae) in colonies of the honey bee *Apis mellifera* L. (Hymenoptera: Apidae) in the northeastern USA. *Journal of Economic Entomology* 98:645–650.
- Calderone, N.W., and M. Nasr. 1999. Evaluation of a formic acid formulation for the fall control of *Varroa jacobsoni* (Acari: Varroidae) in colonies of the honey bee *Apis mellifera* (Hymenoptera: Apidae) in a temperate climate. *Journal of Economic Entomology* 92:526–533.
- Calderone, N.W., and H. Shimanuki. 1995. Evaluation of four seed-derived oils as controls for *Acarapis woodi* (Acari: Tarsonemidae) in colonies of *Apis mellifera* (Hymenoptera: Apidae). *Journal of Economic Entomology* 88:805–809.
- Calderone, N.W., and M. Spivak. 1995. Plant extracts for control of the parasitic mite *Varroa jacobsoni* (Acari: Varroidae) in colonies of the western honey bee (Hymenoptera: Apidae). *Journal of Economic Entomology* 88:1211–1215.
- Calderone, N.W., W.T. Wilson, and M. Spivak. 1997. Plant extracts used for control of the parasitic mites *Varroa jacobsoni* (Acari: Varroidae) and *Acarapis woodi* (Acari: Tarsonemidae) in colonies of *Apis mellifera* (Hymenoptera: Apidae). *Journal of Economic Entomology* 90:1080–1086.
- Camazine, S. 1986. Differential reproduction of the mite, *Varroa jacobsoni* (Mesostigmata: Varroidae), on Africanized and European honey bees (Hymenoptera: Apidae). *Annals of the Entomological Society of America* 79(5):801–803.
- Camazine, S., and R.A. Morse. 1988. The Africanized honeybee. *American Scientist* 76(5):464–471.
- Camerarius, R.J. 1694. Epistola ad M.B. Valentini de sexu plantarum [Letter on the Sexuality of Plants]. In *Ostwald's Klassiker der exakten Naturwissenschaften*, No. 105, 1899. Leipzig: Verlag von Wilhelm Engelmann.
- Cameron, S.A. 2004. Phylogeny and biology of Neotropical orchid bees (Euglossini). *Annual Review of Entomology* 49:377–404.
- Campanhola, C., G. Rodrigues, and B. Dias. 1998. Agricultural biological diversity. *Ciencia e Cultura*, Sao Paulo 50(1):10–12.
- Campbell, B., J. Heraty, J.Y. Rasplus, K. Chan, J. Steffan-Campbell, and C. Babcock. 2000. Molecular systematics of the Chalcidoidea using 28S-rDNA. Pp. 59–73 in *The Hymenoptera: Evolution, Biodiversity and Biological Control*, A.D. Austin and M. Dowton, eds. Canberra: CSIRO Publishing.
- Campbell, D.R., and K.J. Halama. 1993. Resource and pollen limitations to lifetime seed production in a natural plant population. *Ecology* 74:1043–1051.
- Campbell, D.R., and A.F. Motten. 1985. The mechanism of competition for pollination between 2 forest herbs. *Ecology* 66(2):554–563.

- Campbell, N.A., J.B. Reece, and L.G. Mitchell. 1999. *Biology* (5th ed.). California: Benjamin Cummings Publishing Company, Inc.
- Cane, J.H. 1991. Soils of ground-nesting bees (Hymenoptera: Apoidea): texture, moisture, cell depth and climate. *Journal of the Kansas Entomological Society* 64(4):406–413.
- Cane, J.H. 2002. Pollinating bees (Hymenoptera: Apiformes) of U.S. alfalfa compared for rates of pod and seed set. *Journal of Economic Entomology* 95(1):22–27.
- Cane, J.H. 2003. Exotic non-social (Hymenoptera: Apoidea) bees in North America. Pp. 113–126 in *For Nonnative Crops, Whence Pollinators of the Future?*, K. Strickler and J.H. Cane, eds. Proceedings, Entomological Society of America. Lanham, Md.: Thomas Say Publications in Entomology.
- Cane, J.H. 2005. Pollination potential of the bee *Osmia aglaia* for cultivated red raspberries and blackberries (Rubus: Rosaceae). *HortScience* 40(6):1705–1708.
- Cane, J.H., and J.A. Payne. 1988. Foraging ecology of the bee *Habropoda laboriosa* (Hymenoptera: Anthophoridae), an oligolege of blueberries (Ericaceae: Vaccinium) in the Southeastern United States. *Annals of the Entomological Society of America* 81:419–427.
- Cane, J.H., and J.A. Payne. 1990. Native bee pollinates rabbiteye blueberry. *Alabama Agricultural Experiment Statistics* 37:4.
- Cane, J.H., R.L. Minckley, and L.J. Kervin. 2000. Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: pitfalls of pan-trapping. *Journal of the Kansas Entomological Society* 73:225–231.
- Cane, J.H., R.L. Minckley, L.J. Kervin, T.H. Roulston, and N.M. Williams. 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecological Applications* 16:632–644.
- Caron, D.M., and J. Hubner. 2001. 2001 winter loss survey. *American Bee Journal* 141:778–779.
- Carroll, L.E., I.M. White, A. Freidberg, A.L. Norrbom, M.J. Dallwitz, and E.C. Thompson. 2005. *Pest Fruit Flies of the World*. Available at: http://delta-intkey.com/ffa/www/_wintro.htm.
- Carthew, S.M., and R.L. Goldingay. 1997. Non-flying mammals as pollinators. *Trends in Ecology and Evolution* 12:104–108.
- Carvell, C., W.R. Meek, R.F. Pywell, and M. Nowakowski. 2004. The response of foraging bumblebees to successional change in newly created arable field margins. *Biological Conservation* 118:327–339.
- Caspersen, J.P., S.W. Pacala, J.C. Jenkins, G.C. Hurtt, P.R. Moorcroft, and R.A. Birdsey. 2000. Contributions of land-use history to carbon accumulation in U.S. forests. *Science* 290:1148–1151.
- CBD (Convention on Biological Diversity). 2005. *Agricultural Biodiversity: International Initiative for the Conservation and Sustainable Use of Pollinators*. Available at: <http://www.biodiv.org/programmes/areas/agro/pollinators.asp>. Accessed July 24, 2006.
- Ceballos, G., and G. Oliva. 2005. *Los Mamíferos Silvestres de México*. Ed. Fondo de Cultura Económica and Conabio. Mexico D.F., 1986 pp.
- Ceballos, G., T.H. Fleming, C. Chavez, and J. Nassar. 1997. Population dynamics of *Leptonyc-teris curasoe* (Chiroptera: Phyllostomidae) in Jalisco, Mexico. *Journal of Mammalogy* 78:1220–1230.
- Chacoff, N., and M. Aizen. 2006. Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. *Journal of Applied Ecology* 43(1):18–27.
- Charlesworth, D., and B. Charlesworth. 1987. Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* 18:237–268.
- Chen, Y.P., J.A. Higgins, and M.F. Feldlaufer. 2005. Quantitative real-time reverse transcription-CR analysis of deformed wing virus infection in the honeybee (*Apis mellifera* L.). *Applied and Environmental Microbiology* 71:436–441.

- Clark, K.J. 1990. Field trials comparing vegetable oil and menthol as a control for tracheal mites. *American Bee Journal* 130:799–800.
- Clark-Tapia, R., and F. Molina-Freaner. 2004. Reproductive ecology of the rare clonal cactus *Stenocereus eruca* in the Sonoran desert. *Plant Systematics and Evolution* 247:155–164.
- Clay, J. 2004. *World Agriculture and the Environment*. Washington: Island Press.
- Clinebell II, R.R., A. Crowe, D.P. Gregory, and P.C. Hoch. 2004. Pollination ecology of *Gaura* and *Calylophus* (Onagraceae, tribe Onagreae) in western Texas, U.S.A. *Annals of the Missouri Botanical Garden* 91:369–400.
- Cockrum, E.L., and Y. Petryszyn. 1991. The Long-Nosed Bat, *Leptonycteris*: An Endangered Species in the Southwest? Occasional Paper OP-142. Lubbock, Tex.: Museum of Texas Tech University, NSRL Publications.
- Colla, S.R., M.C. Otterstatter, R.J. Gegear, and J.D. Thomson. 2006. Plight of the bumble bee: pathogen spillover from commercial to wild populations. *Biological Conservation* 129:461–467.
- Collins, A.M. 2000. Survival of honey bee (Hymenoptera: Apidae) spermatozoa stored above-freezing temperatures. *Journal of Economic Entomology* 93(3):568–571.
- Collins, A.M. 2004. Sources of variation in the viability of honey bee, *Apis mellifera* L., semen collected for artificial insemination. *Invertebrate Reproduction and Development* 45(3):231–237.
- Collins, A.M., and J.S. Pettis. 2001. Effect of varroa infestation on semen quality. *American Bee Journal* 141:590–593.
- Collins, S.A., G.E. Robinson, and J.K. Conner. 1997. Foraging behavior of honey bees (Hymenoptera: Apidae) on *Brassica nigra* and *B. rapa* grown under simulated ambient and enhanced UV-B radiation. *Annals of the Entomological Society of America* 90(1):102–106.
- Colwell, R.K. 2005. EstimateS, Version 7.5: statistical estimation of species richness and shared species from samples (Software and User's Guide). Freeware published at <http://viceroy.eeb.uconn.edu/estimates>.
- Colwell, R.K., C.X. Mao, and J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85:2717–2727.
- Comins, H.N. 1986. Tactics for resistance management using multiple pesticides. *Agriculture Ecosystems and Environment* 16(2):129–148.
- Condon, M. 1995. Biodiversity, systematics, and Tom Sawyer science. *Conservation Biology* 9:711–714.
- Congressional Research Service. 2006. Reauthorization of the Endangered Species Act (ESA): A Comparison of Pending Bills and a Proposed Amendment with Current Law. Washington: Library of Congress.
- Cook, J.M. 1993. Sex determination in the hymenoptera: a review of models and evidence. *Heredity* 71:421–435.
- Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R.V. O'Neill, J. Paruelo, R.G. Raskin, P. Sutton, and M. van den Belt. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387:253–260.
- Council of Economic Advisers. 2006. Economic report of the President, February 13, 2006. Available at: <http://www.whitehouse.gov/cea/erp06.pdf>. Accessed March 6, 2006.
- Cox, B., F. Eischen, and H. Graham. 2005. American foulbrood survey in honey bees pollinating California almonds. Part I of three parts—widespread incidence of AFB spores. *American Bee Journal* 145(4):302–304.
- Cox, P.A. 1983. Extinction of the Hawaiian avifauna resulted in a change of pollinators for the ieie, *Freycinetia arborea*. *Oikos* 41:195–199.
- Cox, P.A., and T. Elmqvist. 2000. Pollinator extinction in the Pacific Islands. *Conservation Biology* 14:1237–1239.
- Crane, E. 1983. *The Archaeology of Beekeeping*. London: Duckworth. 260 pp.

- Crane, E. 1990. Bees and Beekeeping. Ithaca, NY: Comstock Publishing Associates.
- Crane, E. 1999. The World History of Beekeeping and Honey Hunting. London: Routledge.
- Crespi, B.J., and D. Yanega. 1995. The definition of eusociality. *Behavioral Ecology* 6(1):109–115.
- Cresswell, J.E., and J.L. Osborne. 2004. The effect of patch size and separation on bumblebee foraging in oilseed rape: implications for gene flow. *Journal of Applied Ecology* 41:539–546.
- Crozier, L. 2003. Winter warming facilitates range expansion: cold tolerance of the butterfly *Atalopedes campestris*. *Oecologia* 135:648–656.
- Cruden, R.W. 1973. Reproductive biology of weedy and cultivated *Mirabilis* (Nyctaginaceae). *American Journal of Botany* 60:802–809.
- Cryan, P.M., and M.A. Bogan. 2003. Recurrence of the long-nosed bat (*Choeronycteris mexicana*) at historical sites in Arizona and New Mexico. *Western North American Naturalist* 63(3):314–319.
- Cunningham, S.A. 2000. Depressed pollination in habitat fragments causes low fruit set. *Proceedings of the Royal Society of London Series B—Biological Sciences* 267:1149–1152.
- D'Antonio, C.M., and P.M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle and global change. *Annual Review of Ecology and Systematics* 23:63–87.
- Daehler, C.S. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics* 34:183–211.
- Dafni, A., and A. Shmida. 1996. The possible ecological implications of the invasion of *Bombus terrestris* (L.) (Apidae) at Mt. Carmel, Israel. Pp. 183–200 in *The Conservation of Bees*, A. Matheson, ed. London: Academic Press.
- Dafni, A., P. Bernhardt, A. Shmida, Y. Ivir, S. Greenbaum, C. O'Toole, and L. Losito. 1990. Red bowl-shaped flowers: convergence for beetle pollination in the Mediterranean region. *Israel Journal of Botany* 39:81–92.
- Dafni, A., P.G. Kevan, and B. Husband, eds. 2005. *Practical Pollination Biology*. Cambridge, Canada: Enviroquest Ltd.
- Dag, A., and D. Eisikowitch. 2000. The effect of carbon dioxide enrichment on nectar production in melons under greenhouse conditions. *Journal of Apicultural Research* 39:88–89.
- Daily, G.C., P.A. Matson, and P.M. Vitousek. 1997. Ecosystem services supplied by soil. Pp. 113–132 in *Nature's Services: Societal Dependence on Natural Ecosystems*, G. Daily, ed. Washington: Island Press.
- Dalton, R. 2005. Alcohol and science: saving the agave. *Nature* 438:1070–1071.
- Daly, H.V. 1966. Biological studies on *Ceratina dallatorreana*, an alien bee in California which reproduces by parthenogenesis (Hymenoptera: Apoidea). *Annals of the Entomological Society of America* 59:1138–1154.
- Daly, H.V., G.E. Bohart, and R.W. Thorp. 1971. Introduction of small carpenter bees into California for pollination. I. Release of *Pithitis smaragdula*. *Journal of Economic Entomology* 64:1145–1150.
- Danielsen, F., N.D. Burgess, and A. Balmford. 2005. Monitoring matters: examining the potential of locally-based approaches. *Biodiversity and Conservation* 14:2507–2542.
- Danka, R.G., and T.E. Rinderer. 1986. Africanized bees and pollination. *American Bee Journal* 126:680–682.
- Danka, R.G., T.E. Rinderer, A.M. Collins, and R.L. Hellmich II. 1987. Responses of Africanized honey bees (Hymenoptera: Apidae) to pollination-management stress. *Journal of Economic Entomology* 80(3):621–624.
- Danka, R.G., J.D. Villa, and N.E. Gary. 1993. Comparative foraging distances of Africanized, European and hybrid honey bees (*Apis mellifera* L.) during pollination of cantaloupe (*Cucumis melo* L.). *Bee Science* 3(1):16–21.

- Dauber, J., M. Hirsch, D. Simmering, R. Waldhardt, A. Otte, and V. Wolters. 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. *Agriculture Ecosystems and Environment* 98:321–329.
- Davenport, T.R.B., W.T. Stanley, E.J. Sargis, D.W. De Luca, N.E. Mpunga, S.J. Machaga, and L.E. Olson. 2006. A new genus of African monkey, *Rungwecebus*: morphology, ecology and molecular phylogenetics. *Science* 312:1378–1381.
- Davies, T.J., T.G. Barraclough, M.W. Chase, P.S. Soltis, D.E. Soltis, and V. Savolainen. 2004. Darwin's abominable mystery: insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences, USA* 101(7):1904–1909.
- Davis, A.R. 2003. Influence of elevated CO₂ and ultraviolet-B radiation levels on floral nectar production: a nectary-morphological perspective. *Plant Systematics and Evolution* 238:169–181.
- Day, L. Forthcoming (in prep). *Field Guide to Bumblebees of Illinois and the Eastern United States*.
- de Ruijter, A. 1997. Commercial bumblebee rearing and its implications. Pp. 261–269 in *Proceedings of the 7th International Symposium on Pollination*, K.W. Richards, ed. ISHS Acta Horticulturae 437. Belgium: ISHS.
- de Ruijter, A. 2002. Pollinator diversity and sustainable agriculture in the Netherlands. Pp. 67–70 in *Pollinating Bees—The Conservation Link Between Agriculture and Nature*, P. Kevan and V.L. Imperatriz Fonseca, eds. Brasilia: Ministry of Environment.
- Dedej, S., K.S. Delaplane, and H. Scherm. 2004. Effectiveness of honey bees in delivering the biocontrol agent *Bacillus subtilis* to blueberry flowers to suppress mummy berry disease. *Biological Control* 31:422–427.
- Degenhardt, S., and S. Gronemann. 1988. *Die Zahlungsbereitschaft von Urlaubsgästen für den Naturschutz: Theorie und Empirie des Embeddings-Effektes*. Frankfurt: Lang. 353+21 pp.
- DeGrandi-Hoffman, G., and J.C. Watkins. 2000. The foraging activity of honey bees *Apis mellifera* and non-*Apis* bees on hybrid sunflowers (*Helianthus annuus*) and its influence on cross-pollination and seed set. *Journal of Apicultural Research* 39(1–2):37–45.
- DeJong, D. 1990. Mites: varroa and other parasites of brood. Pp. 200–218 in *Honey Bee Pests, Predators, and Diseases*, R.A. Morse and R. Nowogrodzki, eds. 2nd edition. Ithaca: Cornell University Press.
- DeJong, D. 1996. Africanized honey bees in Brazil, forty years of adaptation and success. *Bee World* 77(2):67–70.
- DeJong, D., and P.H. DeJong. 1983. Longevity of Africanized honey bees (Hymenoptera: Apidae) infested by *Varroa jacobsoni* (Parasitiformes: Varroidae). *Journal of Economic Entomology* 76:766–768.
- DeJong, D., P.H. DeJong, and L.S. Goncalves. 1982a. Weight loss and other damage to developing worker honey bees from infestation with *Varroa jacobsoni*. *Journal of Apicultural Research* 21:165–167.
- DeJong, D., R.A. Morse, and G.C. Eickwort. 1982b. Mite pests of honeybees *Apis* spp., *Varroa jacobsoni*, *Acarapis woodi*, *Tropilaelaps clareae*. *Annual Review of Entomology* 27:229–252.
- DeJong, D., L.S. Goncalves, and R.A. Morse. 1984. Dependence on climate of the virulence of *Varroa jacobsoni*. *Bee World* 65:117–121.
- Delaplane, K.S. 1992. Controlling tracheal mites (Acari: Tarsonemidae) in colonies of honey bees (Hymenoptera: Apidae) with vegetable oil and menthol. *Journal of Economic Entomology* 85:2118–2124.
- Delaplane, K.S., and D.F. Mayer. 2000. *Crop Pollination by Bees*. Oxon: CAB International.
- Delfinado-Baker, M. 1984. *Acarapis woodi* in the United States. *American Bee Journal* 124:805–806.

- Delfinado-Baker, M. 1988. The tracheal mite of honey bees: a crisis in beekeeping. Pp. 493–497 in *Africanized Honey Bees and Bee Mites*, G.R. Needham, R.E. Page, Jr., M. Delfinado-Baker, and C.E. Bowman, eds. Chichester: Halsted Press.
- Delpino, F. 1868–1875. Ulteriori osservazione sulla dicogamia nel regno vegetale. *Atti della Societa Italiana di Scienze Naturali Milano*, Vols. 1 and 2.
- Demauro, M.M. 1993. Relationship of breeding system to rarity in the lakeside daisy (*Hymenoxys acaulis* var. *glabra*). *Conservation Biology* 7:542–550.
- Dhondt, A.A., S. Altizer, E.G. Cooch, A.K. Davis, A. Dobson, M.J.L. Driscoll, B.K. Hartup, D.M. Hawley, W.M. Hochachka, P.R. Hosseini, C.S. Jennelle, G.V. Kollias, D.H. Ley, E.C.H. Swarthout, and K.V. Sydenstricker. 2005. Dynamics of a novel pathogen in an avian host: mycoplasmal conjunctivitis in house finches. *Acta Tropica* 94:77–93.
- Dias, B.S.F., A. Raw, and V.L. Imperatri-Fonsec. 1999. International Pollinators: Initiative: The São Paulo Declaration on Pollinators. Report on the Recommendations of the Workshop on Conservation and Sustainable Use of Pollinators in Agriculture with Emphasis on Bees. Available at: <http://www.rge.fmrp.usp.br/beescience/arquivospdf/workshop.pdf>. Accessed May 31, 2006.
- Dick, C.W. 2001. Genetic rescue of remnant tropical trees by an alien pollinator. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences* 268:2391–2396.
- Dietz, A., and C. Vergara. 1995. Africanized honey bees in temperate zones. *Bee World* 76(2):56–71.
- Dilley, J.D. 2000. The radiation of *Calochortus*: generalist flowers moving through a mosaic of potential pollinators. *Oikos* 89:209–222.
- Dixon, D.P., and B.G. Fingler. 1982. The effects of the 1981 Manitoba emergency mosquito control program on honey bees. Pp. 243–247 in *Western Equine Encephalitis in Manitoba*. Winnipeg: Government of Manitoba.
- Dixon, D.P., and B.G. Fingler. 1984. The effects of the mosquito control program on bees. Pp. 101–121 in *Final Technical Report on Environmental Monitoring Program for the 1983 Spraying of Malathion to Combat Western Equine Encephalitis*. Winnipeg: Government of Manitoba.
- Dobson, A., D. David Lodge, J. Alder, G.S. Cumming, J. Keymer, J. McGlade, H. Mooney, J.A. Rusak, O. Sala, V. Wolters, D. Wall, R. Winfree, and M.A. Xenopoulos. 2006. Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology* 87(8):1915–1924.
- Dodson, C.H., R.L. Dressler, H.G. Hills, R.M. Adams, and N.H. Williams. 1969. Biologically active compounds in orchid fragrances. *Science* 164:1243–1249.
- Dodson, M., J. Bachmann, and P. Williams. 2002. Organic Greenhouse Tomato Production. ATTRA Publication #IP190/197. Available at: <http://www.attra.org/attra-pub/ghtomato.html>.
- Dogterom, M.H., and M.L. Winston. 1999. Pollen storage and foraging by honey bees (Hymenoptera: Apidae) in highbush blueberries (Ericaceae), cultivar Bluecrop. *Canadian Entomology* 31:757–768.
- Donaldson, J.S. 2002. Pollination in agricultural landscapes, a South African perspective. Pp. 97–104 in *Pollinating Bees—The Conservation Link Between Agriculture and Nature*, P. Kevan and V.L. Imperatriz Fonseca, eds. Brasilia: Ministry of Environment.
- Donzella, G., A. Spena, and G.L. Rotino. 2000. Transgenic parthenocarpic eggplants: superior germplasm for increased winter production. *Molecular Breeding* 6(1):79–86.
- Dover, J.W. 1991. The conservation of insects on arable farmland. Pp. 294–318 in *The Conservation of Insects and Their Habitats*, N.M. Collins and J.A. Thomas, eds. Symposium of the Royal Entomological Society of London, 15. London: Academic Press.
- Duay, P., D. De Jong, and W. Engels. 2002. Decreased flight performance and sperm production in drones of the honey bee (*Apis mellifera*) slightly infested by *Varroa destructor* mites during pupal development. *Genetics and Molecular Research* 1:227–232.

- Dudash, M.R. 1990. Relative fitness of selfed and outcrossed progeny in a self-compatible, protandrous species, *Sabatia angularis* L. (Gentianaceae)—a comparison in three environments. *Evolution* 44:1129–1139.
- Duff, S.R., and B. Furgala. 1993. Evaluation of amitraz and menthol as agents to control honey bee tracheal mite infestations in non-migratory honey bee colonies in Minnesota. *American Bee Journal* 133(2):127–130.
- Dukas, R., and P.K. Visscher. 1994. Lifetime learning by foraging honey bees. *Animal Behavior* 48:1007–1012.
- Duncan, D.H., A.B. Nicotra, J.T. Wood, and S.A. Cunningham. 2004. Plant isolation reduces outcross pollen receipt in a partially self-compatible herb. *Journal of Ecology* 92:977–985.
- Dupont, Y.L., D.M. Hansen, A. Valido, and J.M. Olesen. 2004. Impact of introduced honey bees on native pollination interactions of the endemic *Echium wildpretii* (Boraginaceae) on Tenerife, Canary Islands. *Biological Conservation* 118:301–311.
- Eardley, C., D. Roth, J. Clarke, S. Buchman, and B. Gemmill, eds. 2006. *Pollinators and Pollination: A Resource Book for Policy and Practice*. Pretoria: African Pollinator Initiative. 77 pp.
- Ehrenfeld, J.G., and L.A. Toth. 1997. Restoration ecology and the ecosystem perspective. *Restoration Ecology* 5(4):307–317.
- Ehrlich, P.R., and I. Hanski, eds. 2004. *On the Wings of Checkerspots: A Model System for Population Biology*. New York: Oxford University Press.
- Ehrlich, P.R., D.S. Dobkin, and D. Wheye. 1988. *The birder's handbook*. New York: Simon and Schuster.
- Eickwort, G.C. 1980. Two European species of *Chelostoma* established in New York State (Hymenoptera: Megachilidae). *Psyche* 87:315–323.
- Eischen, F.A. 1987. Overwintering performance of honey bee colonies heavily infested with *Acarapis woodi* (Rennie). *Apidologie* 18(4):293–303.
- Eischen, F.A., D. Cardoso-Tamez, W.T. Wilson, and A. Dietz. 1989. Honey production of honey bee colonies infested with *Acarapis woodi* (Rennie). *Apidologie* 20(1):1–8.
- Eischen, F.A., W.T. Wilson, J.S. Pettis, A. Suarez, D. Cardoso-Tamez, D.L. Maki, A. Dietz, J. Vargas, C.G. Estrada, and W.L. de Rubink. 1990. TI: The spread of *Acarapis woodi* (Acari: Tarsonemidae) in northeastern Mexico. *Journal of the Kansas Entomological Society* 63(3):375–384.
- Ellis, J.D., Jr., K.S. Delaplane, and W.M. Hood. 2001. Efficacy of bottom screen devices, Apistan™, and Apilife VAR™ in controlling *Varroa destructor*. *American Bee Journal* 141:813–816.
- Ellis, J.D., Jr., I.H. Rong, M.P. Hill, H.R. Hepburn, and P.J. Elzen. 2004a. The susceptibility of small hive beetle (*Aethina tumida* Murray) pupae to fungal pathogens. *American Bee Journal* 144:486–488.
- Ellis, J.D., Jr., R. Hepburn, B. Luckman, and P.J. Elzen. 2004b. Effects of soil type, moisture, and density on pupation success of *Aethina tumida* (Coleoptera: Nitidulidae). *Environmental Entomology* 33(4):794–798.
- Ellstrand, N.C., and E.R. Elam. 1993. Population genetic consequences of small population size: implications for plant conservation. *Annual Review of Ecology and Systematics* 24:217–242.
- Elzen, P.J., and D. Westervelt. 2002. Detection of coumaphos resistance in *Varroa destructor* in Florida. *American Bee Journal* 142:291–292.
- Elzen, P.J., F.A. Eischen, J.B. Baxter, J.S. Pettis, G.W. Elzen, and W.T. Wilson. 1998. Fluvalinate resistance in *Varroa jacobsoni* from several geographic locations. *American Bee Journal* 138:674–676.
- Elzen, P.J., J.R. Baxter, F.A. Eischen, and W.T. Wilson. 1999a. Pesticide resistance in *Varroa* mites: theory and practice. *American Bee Journal* 139(3):195–196.

- Elzen, P.J., J.R. Baxter, D. Westervelt, C. Randall, K.S. Delaplane, L. Cutts, and W.T. Wilson. 1999b. Field control and biology studies of a new pest species, *Aethina tumida* Murray (Coleoptera, Nitidulidae), attacking European honey bees in the Western Hemisphere. *Apidologie* 30(5):361–366.
- Elzen, P.J., F.A. Eischen, J.R. Baxter, G.W. Elzen, and W.T. Wilson. 1999c. Detection of resistance in US *Varroa jacobsoni* Oud. (Mesostigmata:Varroidae) to the acaricide flouvalinate. *Apidologie* 30:13–17.
- Elzen, P.J., J.R. Baxter, M. Spivak, and W.T. Wilson. 1999d. Amitraz resistance in *Varroa*: new discovery in North America. *American Bee Journal* 139(5):362.
- Elzen, P.J., J.R. Baxter, M. Spivak, and W.T. Wilson. 2000. Control of *Varroa jacobsoni* Oud. resistant to flouvalinate and amitraz using coumaphos. *Apidologie* 31(3):437–441.
- Elzen, P.J., J.R. Baxter, P. Neumann, A. Solbrig, C. Pirk, H.R. Hepburn, D. Westervelt, and C. Randall. 2001. Behaviour of African and European subspecies of *Apis mellifera* toward the small hive beetle, *Aethina tumida*. *Journal of Apicultural Research* 40(1):40–41.
- Elzen, P.J., D. Westervelt, D. Causey, R. Rivera, J. Baxter, and M. Feldlaufer. 2002. Control of oxytetracycline-resistant American foulbrood with tylosin and its toxicity to honey bees (*Apis mellifera*). *Journal of Apicultural Research* 41:97–100.
- Elzinga, C.L., D.W. Salzer, J.W. Willoughby, and J.P. Gibbs. 2001. *Monitoring Plant and Animal Populations*. Malden, Mass.: Blackwell Science Inc.
- Endress, P.K. 1994. *Diversity and Evolutionary Biology of Tropical Flowers*. Cambridge: Cambridge University Press. 511 pp.
- Engels, W., and K. Schatton. 1986. Changes in hemolymph proteins and weight loss in worker bees due to varroa parasitization. *Arbeitsgemeinschaft der Institute für Bienenforschung E.V. Abstracts of the Varroa Workshop in Feldafing/Starnberg, West Germany*.
- Engels, W., U. Schultz, and M. Radle. 1994. Use of the Tübingen mix for bee pasture in Germany. Pp. 57–65 in *Forage for Bees in an Agricultural Landscape*, A. Matheson, ed. Cardiff: International Bee Research Association.
- Erickson, J.L., and S.D. West. 2003. Associations of bats with local structure and landscape features of forested stands in western Oregon and Washington. *Biological Conservation* 109:95–102.
- Erwin, T.L. 1982. Tropical forests: their richness in *Coleoptera* and other arthropod species. *The Coleopterist's Bulletin* 36:74–75
- Erwin T.L. 2004. The biodiversity question: How many species of terrestrial arthropods are there? Pp. 259-269 in *Forest Canopies*, 2nd edition, M.D.L. Lowman, and H.B. Rinker, eds. Burlington, Vt.: Elsevier Academic Press.
- Estrada, C., and C.D. Jiggins. 2002. Patterns of pollen feeding and habitat preference among *Heliconius* species. *Ecological Entomology* 27:448–456.
- Etcheverry, A.V., and C.E.T. Aleman. 2005. Reproductive biology of *Erythrina falcata* (Fabaceae: Papilionoideae). *Biotropica* 37:54–63.
- Evans, J.D. 2003. Diverse origins of tetracycline resistance in the honey bee bacterial pathogen *Paenibacillus larvae*. *Journal of Invertebrate Pathology* 83:46–50.
- Evelyn, M.J., D.A. Stiles, and R.A. Young. 2004. Conservation of bats in suburban landscapes: roost selection by *Myotis yumanensis* in a residential area in California. *Biological Conservation Newsletter* 115(3):463–473.
- Faegri, K., and L. van der Pijl. 1966. *The Principles of Pollination Biology*. New York: Pergamon Press.
- Faegri, K., and L. van der Pijl. 1979. *The Principles of Pollination Ecology*. 3rd edition. Oxford: Pergamon Press.
- FAO (Food and Agriculture Organization of the United Nations). 2005. FAOSTAT Online. Available at: <http://apps.fao.org>. Accessed January 2005.
- Farrar, K. 1999. Crop Profile for Figs in California. Available at: <http://pestdata.ncsu.edu/cropprofiles/docs/cafigs.html>. Accessed March 22, 2006.

- Farrell, B.D., and C. Mitter. 1993. Phylogenetic determinants of insect/plant community diversity. Pp. 253–266 in *Species Diversity: Historical and Geographical Perspectives*, R.E. Ricklefs and D. Schluter, eds. Chicago: University of Chicago Press.
- Feldlaufer, M.F., J.S. Pettis, J.P. Kochansky, and H. Shimanuki. 1997. A gel formulation of formic acid for the control of parasitic mites of honey bees. *American Bee Journal* 137(9):661–663.
- Fenster, C.B., and M.R. Dudash. 2001. Spatiotemporal variation in the role of hummingbirds as pollinators of *Silene virginica*. *Ecology* 82:844–851.
- Fenster, C.B., S. Armbruster, P. Wilson, M. Dudash, and J.D. Thomson. 2004. Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution, and Systematics* 35:375–403.
- Fenton, M.B. 1997. Science and the conservation of bats. *Journal of Mammalogy* 78:1–14.
- Finley, J., S. Camazine, and M. Frazier. 1996. The epidemic of honey bee colony losses during the 1995–1996 season. *American Bee Journal* 136:805–808.
- Fisher, R.M., and N. Pomeroy. 1989. Incipient colony manipulation, Nosema incidence and colony productivity of the bumble bee *Bombus terrestris* (Hymenoptera, Apidae). *Journal of the Kansas Entomological Society* 62:581–589.
- Flanders, K.L., and E.B. Radcliff. 2000. Alfalfa IPM. Available at: <http://ipmworld.umn.edu/chapters/flanders.htm>. Accessed May 17, 2006.
- Flanders, R.V., W.F. Wehling, and A.L. Craghead. 2003. Laws and regulations on the import, movement, and release of bees in the United States. Pp. 99–111 in *For Nonnative Crops, Whence Pollinators of the Future?*, K. Strickler and J.H. Cane, eds. Proceedings, Entomological Society of America. Lanham, Md.: Thomas Say Publications in Entomology.
- Fleishman, E., J.R. Thomson, R. MacNally, D.D. Murphy, and J.P. Fay. 2005. Using indicator species to predict species richness of multiple taxonomic groups. *Conservation Biology* 19:1125–1137.
- Fleming, T.H. 2000. Pollination of cacti in the Sonoran Desert. *American Scientist* 88:432–439.
- Fleming, T.H. 2004. Nectar corridors. Migration and the annual cycle of lesser long-nosed bats. Pp. 23–42 in *Conservation of Migratory Pollinators and Their Nectar Corridors in North America*, G. Nabhan, R.C. Brusca, and L. Holter, eds. Arizona–Sonora Desert Museum, Natural History of the Sonoran Desert Region, No. 2. Tucson: University of Arizona Press.
- Fleming, T.H., and J.N. Holland. 1998. The evolution of obligate pollination mutualisms: senita cactus and senita moth. *Oecologia* 114:368–375.
- Fleming, T.H., and J. Nassar. 2002. The population biology of a nectar-feeding bat, *Leptonycteris curasoae*, in Mexico and northern South America. Pp. 283–305 in *Columnar Cacti and Their Mutualists: Evolution, Ecology, and Conservation*, T.H. Fleming and A. Valiente-Banuet, eds. Tucson: University of Arizona Press.
- Fleming, T.H., R.A. Nunez, and L. Sternberg. 1993. Seasonal changes in the diets of migrant and non-migrant nectarivorous bats as revealed by carbon stable isotope analysis. *Oecologia* 94:72–75.
- Fleming, T.H., T. Tibbitts, Y. Petryszyn, and V. Dalton. 2001a. Current status of pollinating bats in the southwestern United States. In *Monitoring Bat Populations in the United States*, T. O’Shea and M. Bogan, eds. Fort Collins: U.S. Geological Survey.
- Fleming, T.H., C.T. Sahley, J.N. Holland, J.D. Nason, and J.L. Hamrick. 2001b. Sonoran Desert columnar cacti and the evolution of generalized pollination systems. *Ecological Monographs* 71:511–530.
- Flores, J.M., J.A. Ruiz, J.M. Ruz, F. Puerta, M. Bustos, F. Padilla, and F. Campano. 1996. Effect of temperature and humidity of sealed brood on chalkbrood development under controlled conditions. *Apidologie* 27:185–192.
- Flottum, K. 2005. Inner cover. *Bee Culture* 133:10, 49.

- Fontaine, C., I. Dajoz, J. Meriguet, and M. Loreau. 2006. Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. *PLoS Biology* 4:129–135.
- Forister, M.L., and A.M. Shapiro. 2003. Climatic trends and advancing spring flight of butterflies in lowland California. *Global Change Biology* 9:1130–1135.
- Forup, M.L., and J. Memmott. 2005. The restoration of plant-pollinator interactions in hay meadows. *Restoration Ecology* 13:265–274.
- Forys, E., and C.R. Allen. 2005. The impacts of sprawl on biodiversity: the ant fauna of the lower Florida Keys. *Ecology and Society* 10(1):25.
- Frank, G., ed. 2003. *Alfalfa Seed and Leafcutter Bee Production and Marketing Manual*. Brooks, Alberta: Irrigated Alfalfa Seed Producers Association. 160 pp.
- Frankie, G.W., R.W. Thorp, L.E. Newstrom-Lloyd, M.A. Rizzardi, J.F. Barthell, T.L. Griswold, J.-Y. Kim, and S. Kappagoda. 1998. Monitoring solitary bees in modified wildland habitats: implications for bee ecology and conservation. *Environmental Entomology* 27:1137–1148.
- Frankie, G.W., R.W. Thorp, M. Schindler, J. Hernandez, B. Ertter, and M. Rizzardi. 2005. Ecological patterns of bees and their host ornamental flowers in two northern California cities. *Journal of the Kansas Entomological Society* 78:227–246.
- Franklin, M.T., M.L. Winston, and L.A. Morandin. 2004. Effects of clothianidin on *Bombus impatiens* (Hymenoptera: Apidae) colony health and foraging ability. *Journal of Economic Entomology* 97(2):369–373.
- Frazier, M.T., J. Finley, C.H. Collison, and E. Rajotte. 1994. The incidence and impact of honey bee tracheal mites and nosema disease on colony mortality in Pennsylvania. *Bee Science* 3:94–100.
- Free, J.B. 1970. *Insect Pollination of Crops*. New York: Academic Press.
- Free, J.B. 1993. *Insect Pollination of Crops*. 2nd edition. San Diego: Academic Press.
- Freitas, B.M., and J.O.P. Pereira, eds. 2004. *Solitary Bees—Conservation, Rearing and Management for Pollination*. Fortaleza: Imprensa Universitária.
- Frick, T.B., and D.W. Tallamy. 1996. Density and diversity of nontarget insects killed by suburban electric insect traps. *Entomological News* 107:77–82.
- Fries, I., S. Camazine, and J. Sneyd. 1994. Population dynamics of *Varroa jacobsoni*: a model and a review. *Bee World* 75:5–28.
- Frison, T.H. 1921. New distribution records for North American Bremidae, with the description of a new species (Hym). *Entomology News* 32:144–148.
- Fronk, W.D. 1963. Increasing alkali bees for pollination. Wyoming Agricultural Experimental Station Mimeo Circular 184.
- Gaidet-Drapier, N., H. Fritz, M. Bourgarel, P.C. Renaud, P. Poilecot, P. Chardonnet, C. Coid, D. Poulet, and S. Le Bel. 2006. Cost and efficiency of large mammal census techniques: comparison of methods for a participatory approach in a communal area, Zimbabwe. *Biodiversity and Conservation* 15:735–754.
- Galen, C., K.A. Zimmer, and M.E. Newport. 1987. Pollination in floral scent morphs of *Polemonium viscosum*: a mechanism for disruptive selection on flower size. *Evolution* 41:599–606.
- Galindo, C., A. Sanchez, R.H. Quijano, and L.G. Herrera. 2004. Population dynamics of a resident colony of *Leptonycteris curasoae* (Chiroptera: Phyllostomidae) in central Mexico. *Biotropica* 36:382–391.
- Gary, N.E., R.E. Page, Jr., R.A. Morse, C.E. Henderson, M.E. Nasr, and K. Lorenzen. 1990. Comparative resistance of honey bees (*Apis mellifera* L.) from Great Britain and United States to infestation by tracheal mites (*Acarapis woodi*). *American Bee Journal* 130:667–669.

- Gathmann, A., H.J. Greiler, and T. Tsharntke. 1994. Trap-nesting bees and wasps colonizing set-aside fields: succession and body size, management by cutting and sowing. *Oecologia* 98:8–14.
- Gegeer, R.J., M.C. Otterstatter, and J.D. Thomson. 2005. Does parasitic infection impair the ability of bumblebees to learn flower-handling techniques? *Animal Behaviour* 70:209–215.
- Gels, J.A., D.W. Held, and D.A. Potter. 2002. Hazards of insecticides to the bumble bees *Bombus impatiens* (Hymenoptera: Apidae) foraging on flowering white clover in turf. *Journal of Economic Entomology* 95(4):722–728.
- Genersch E., C. Yue, I. Fries, and J.R. de Miranda. 2006. Detection of deformed wing virus, a honey bee viral pathogen, in bumble bees (*Bombus terrestris* and *Bombus pascuorum*) with wing deformities. *Journal of Invertebrate Pathology* 91(1):61–63.
- Georghiou, G.P. 1980. Insecticide resistance and prospects for its management. *Residue Reviews* 76:131–145.
- Gerson, U., R. Mozes-Koch, and E. Cohen. 1991. Enzyme levels used to monitor pesticide resistance in *Varroa jacobsoni*. *Journal of Apicultural Research* 30(1):17–20.
- Gess, F.W., and S.K. Gess. 1993. Effects of increasing land utilization on species representation and diversity of aculeate wasps and bees in the semi-arid areas of southern Africa. Pp. 83–113 in *Hymenoptera and Biodiversity*, J. LaSalle and I.D. Gauld, eds. Wallingford: CAB International.
- Ghazoul, J. 2005a. Buzziness as usual? Questioning the global pollination crisis. *Trends in Ecology and Evolution* 20(7):367–373.
- Ghazoul, J. 2005b. Response to Steffan-Dewenter et al., 2005: Questioning the global pollination crisis. *Trends in Ecology and Evolution* 20(12):652–653.
- Ghazoul, J. 2005c. Pollen and seed dispersal among dispersed plants. *Biological Reviews* 80:413–443.
- Gibbs, D., D. Walton, L.P. Brower, and A.K. Davis. 2006. Monarch butterfly (Lepidoptera, Nymphalidae) migration monitoring at Chincoteague, VA and Cape May, NJ: a comparison of long-term trends. *Journal of the Kansas Entomological Society* 79(2):56–164.
- Giles, V., and J.S. Ascher. 2006. A Survey of the Bees of the Black Rock Forest Preserve, New York (Hymenoptera: Apoidea). *Journal of Hymenoptera Research* 15:208–231.
- Givnish, T.J. 1986. Serotiny, Geography, and Fire in the Pine Barrens of New Jersey. *Evolution* 35:101–123.
- Gochnauer, T.A. 1951. Drugs fight foul brood diseases in bees. *Minnesota Farms and Home Science* 9:15.
- Goettel, M.S., G.M. Duke, and D.W. Goerzen. 1997. Pathogenicity of *Ascospaera larvis* to larvae of the alfalfa leafcutting bee, *Megachile rotundata*. *Canadian Entomologist* 129:1059–1065.
- Goldblatt, P., and J.C. Manning. 1999. *Gladiolus* in Southern Africa. Cape, South Africa: Fernwood Press.
- Goldblatt, P., P. Bernhardt, and J.C. Manning. 1998. Pollination of petaloid geophytes by monkey beetles (Scarabaeidae: Rutelinae: Hoplini) in southern Africa. *Annals of the Missouri Botanical Garden* 85:215–230.
- Goldblatt, P., P. Bernhardt, P. Vogan, and J.C. Manning. 2004. Pollination by fungus gnats (Diptera Myscetophilidae) and self-recognition sites in *Tolmiea menziesii* (Saxifragaceae). *Plant Systematics and Evolution* 244:55–67.
- Goldblatt, P., J.C. Manning, and P. Bernhardt. 2005. The floral biology of *Melaspheerula* (Iridaceae:Crococoidae): is this monotypic genus pollinated by March flies (Diptera: Bibionidae)? *Annals of the Missouri Botanical Garden* 92:268–274.
- Goldingay, R.L., S.M. Carthew, and R.J. Whelan. 1991. The importance of non-flying mammals in pollination. *Oikos* 61:79–87.

- Gómez, J.M. 2000. Effectiveness of ants as pollinators of *Lobularia maritima*: effects on main sequential fitness components of the host plant. *Oecologia* 122:90–97.
- Gómez, J.M., R. Zamora, J.A. Hoda, and D. Garcia. 1996. Experimental study of pollination by ants in Mediterranean high mountain and arid habitats. *Oecologia* 105:236–242.
- Goncalves, L.S., A.C. Stort, and D. DeJong. 1991. Beekeeping in Brazil. Pp. 359–372 in *The “African” Honey Bee*, M. Spivak, D.J.C. Fletcher, and M.D. Breed, eds. Oxford: Westview Press.
- Goodwillie, C. 2000. Inbreeding depression and mating systems in two species of *Linanthus* (Polemoniaceae). *Heredity* 84:283–293.
- Goodwin, M., and C. Van Eaton. 1999. Elimination of American Foulbrood Without the Use of Drugs. National Beekeepers’ Association of New Zealand. Tauranga, New Zealand: Advance Print. 78 pp.
- Gorguet, B., A.W. van Heusden, and P. Lindhout. 2005. Parthenocarpic fruit development in tomato. *Plant Biology* 7(2):131–139.
- Gottsberger, G. 1989a. Beetle pollination and flowering rhythm of *Annona* spp. (Annonaceae) in Brazil. *Plant Systematics and Evolution* 167:165–187.
- Gottsberger, G. 1989b. Comments on flower evolution and beetle pollination in the genera *Annona* and *Rollinia* (Annonaceae). *Plant Systematics and Evolution* 167:189–194.
- Goulson, D. 2003a. Effects of introduced bees on native ecosystems. *Annual Review of Ecology and Systematics* 34:1–26.
- Goulson, D. 2003b. Conserving wild bees for crop pollination. *Food, Agriculture and Environment* 1(1):142–144.
- Goulson, D. 2003c. *Bumblebees: Their Behaviour and Ecology*. New York: Oxford University Press.
- Goulson, D., and L.C. Derwent. 2004. Synergistic interactions between an exotic honeybee and an exotic weed: pollination of *Lantana camara* in Australia. *Weed Research* 44:195–202.
- Goulson, D., M.E. Hanley, B. Darvill, J.S. Ellis, and M.E. Knight. 2005. Causes of rarity in bumblebees. *Biological Conservation* 122:1–8.
- Graham, C.H., S. Ferrier, F. Huettman, C. Moritz, and A.T. Peterson. 2004. New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology and Evolution* 19:497–503.
- Grant, K.A., and V. Grant. 1965. *Flower Pollination in the Phlox Family*. New York: Columbia University Press.
- Grant, K.A., and V. Grant. 1967. Effects of hummingbird migration on plant speciation in the California flora. *Evolution* 21:457–465.
- Grant, K.A., and V. Grant. 1968. *Hummingbirds and their flowers*. New York: Columbia University Press.
- Grant, V. 1950. The pollination of *Calycanthus occidentalis*. *American Journal of Botany* 37:294–297.
- Grant, V. 1985. Additional observations on temperate North American hawkmoth flowers. *Botanical Gazette* 146:517–520.
- Grant, V., and K.A. Grant. 1979. The pollination spectrum in the southwestern american cactus flora. *Plant Systematics and Evolution* 133:29–37.
- Green, M.B., H.M. LeBaron, and W.K. Moberg. 1990. *Managing Resistance to Agrochemicals: from Fundamental Research to Practical Strategies*. Washington: American Chemical Society. 496 pp.
- Greenleaf, S.S. 2005. Local-scale and foraging-scale affect bee community abundances, species richness, and pollination services in Northern California. Ph.D thesis. Princeton University.

- Greenleaf, S.S., and C. Kremen. 2006a. Wild bee species increase tomato production but respond differently to surrounding land use in Northern California. *Biological Conservation* 133:81–87.
- Greenleaf, S.S., and C. Kremen. 2006b. Wild bees enhance pollination by honey bees' pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences USA* 103:13890–13895.
- Gregory, D.P. 1963–1964. Hawkmoth pollination in the genus *Oenothera*. *Aliso* 5:357–419.
- Griffin, B.L. 1993. *The Orchard Mason Bee*. Bellingham: Knox Cellars Publishing. 69 pp.
- Griffin, B.L. 1999. *The Orchard Mason Bee: The Life History, Biology, Propagation and Use of a Truly Benevolent and Beneficial Insect*. Bellingham: Knox Cellars Publishing.
- Griffith, M.P. 2004. The origins of an important cactus crop, *Opuntia ficus-indica* (Cactaceae): new molecular evidence. *American Journal of Botany* 91:1915–1921.
- Grimaldi, D., and M.S. Engel. 2005. *Evolution of the Insects*. New York: Cambridge University Press.
- Grixti, J.C., and Packer, L. 2006. Changes in the bee fauna (Hymenoptera: Apoidea) of an old field site in southern Ontario, revisited after 34 years. *Canadian Entomologist* 138(2):147–164.
- Groom, M.J. 1998. Allee effects limit population viability of an annual plant. *American Naturalist* 151:487–496.
- Groom, M.J. 2001. Consequences of subpopulation isolation for pollination, herbivory, and population growth in *Clarkia concinna* (Onagraceae). *Biological Conservation* 100:55–63.
- Guzmán-Novoa, E., and R.E. Page, Jr. 1994a. The impact of Africanized bees on Mexican beekeeping. *American Bee Journal* 134(2):101–106.
- Guzmán-Novoa, E., and R.E. Page, Jr. 1994b. Genetic dominance and worker interactions affect honeybee colony defense. *Behavioral Ecology* 5(1):91–97.
- Guzmán-Novoa, E., and R.E. Page, Jr. 1999. Selective breeding of honey bees (Hymenoptera: Apidae) in Africanized areas. *Journal of Economic Entomology* 92(3):521–525.
- Hackney, E.E., and J.B. McGraw. 2001. Experimental demonstration of an Allee effect in American ginseng. *Conservation Biology* 1:129–136.
- Hall, R.J., S. Gubbins, and C.A. Gilligan. 2004. Invasion of drug and pesticide resistance is determined by a trade-off between treatment efficacy and relative fitness. *Bulletin of Mathematical Biology* 66(4):825–840.
- Halpern, S. 2001. *Four Wings and a Prayer: Caught in the Mystery of the Monarch Butterfly*. New York: Pantheon.
- Hambler, C., and M.R. Speight. 1996. Extinction rates in British nonmarine invertebrates since 1900. *Conservation Biology* 10:892–896.
- Handel, S.N. 1997. The role of plant-animal mutualisms in the design and restoration of natural communities. Pp. 111–132 in *Restoration Ecology and Sustainable Development*, K.M. Urbanska, N.R. Webb, and P.J. Edwards, eds. Cambridge: Cambridge University Press.
- Handel, S.N., G.R. Robinson, and A.J. Beattie. 1994. Biodiversity resources for restoration ecology. *Restoration Ecology* 2:230–241.
- Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. *Nature* 404:755–758.
- Harbo, J.R. 1992. Breeding honey bees (Hymenoptera; Apidae) for more rapid development of larvae and pupae. *Journal of Economic Entomology* 85(6):2125–2130.
- Harbo, J.R. 1993. Evaluating bees for resistance to *Varroa* mites. *American Bee Journal* 133(12):865.
- Harbo, J.R., and J.W. Harris. 1999a. Selecting honey bees for resistance to *Varroa jacobsoni*. *Apidologie* 30(2–3):183–196.

- Harbo, J.R., and J.W. Harris. 1999b. Heritability in honey bees (Hymenoptera: Apidae) of characteristics associated with resistance to *Varroa jacobsoni* (Mesostigmata: Varroidae). *Journal of Economic Entomology* 92(2):261–265.
- Harbo, J.R., and J.W. Harris. 2001. Resistance to *Varroa destructor* (Mesostigmata: Varroidae) when mite-resistant queen honey bees (Hymenoptera: Apidae) were free-mated with unselected drones. *Journal of Economic Entomology* 94(6):1319–1323.
- Harbo, J.R., and J.W. Harris. 2004. Effect of screen floors on populations of honey bees and parasitic mites (*Varroa destructor*). *Journal of Apicultural Research* 43(3):114–117.
- Harbo, J.R., and J.W. Harris. 2005. Suppressed mite reproduction explained by the behaviour of adult bees. *Journal of Apicultural Research* 44(1):21–23.
- Harbo, J.R., and R. Hoopingarner. 1995. Resistance to varroa expressed by honey bees in the USA. *American Bee Journal* 135(12):827.
- Harbo, J.R., R.A. Hoopingarner, and J.W. Harris. 1997. Evaluating honey bees for resistance to varroa mites: procedures and results. *American Bee Journal* 137(3):223–224.
- Harder, L.D. 1982. Functional differences of the proboscides of short- and long-tongued bees (Hymenoptera, Apidae). *Candian Journal of Zoology* 61:1580–1586.
- Harder, L.D. 1983. Flower handling efficiency of bumble bees: morphological aspects of probing time. *Oecologia* 57(1–2):274–280.
- Harder, L.D. 1986. Effects of nectar concentration and flower depth on flower handling efficiency of bumble bees. *Oecologia* 69:309–315.
- Harris, J.W., and T.E. Rinderer. 2004. *Varroa* resistance of hybrid ARS Russian honey bees. *American Bee Journal* 144:797–800.
- Harris, J.W., T. Rinderer, V. Kuznetsov, R. Danka, G. Delatte, L. de Guzman, and J. Villa. 2002. Imported Russian honey bees: quarantine and initial selection for varroa resistance. *American Bee Journal* 142:591–596.
- Harris, L.F., and S.D. Johnson. 2004. The consequences of habitat fragmentation for plant-pollinator mutualisms. *International Journal of Tropical Insect Science* 24:29–43.
- Harrison, S., and L. Fahrig. 1995. Landscape pattern and population conservation. Pp. 293–308 in *Mosaic Landscapes and Ecological Processes*, L. Hansson, L. Fahrig, and G. Merriam, eds. New York: Chapman and Hall.
- Harrison, S., D.D. Murphy, and P.R. Ehrlich. 1988. Distribution of the bay checkerspot butterfly, *Euphydryas Editha Bayensis*: evidence for a metapopulation model. *American Naturalist* 132:360–382.
- Hartl, D.L., and A.G. Clark. 1997. *Principles of Population Genetics*. 3rd edition. Sunderland, Mass.: Sinauer Associates.
- Haseman, L., and L.F. Childers. 1944. Controlling American foulbrood with sulfa drugs. *Missouri Agricultural Experimentation Station Bulletin* 482:1–16.
- Haugaasen, T., J. Barlow, and C.A. Peres. 2003. Effects of surface fires on understory insectivorous birds and terrestrial arthropods in central Brazilian Amazonia. *Animal Conservation* 6:299–306.
- Haughton, A.J., G.T. Champion, C. Hawes, M.S. Heard, D.R. Brooks, D.A. Bohan, S.J. Clark, A.M. Dewar, L.G. Firbank, J.L. Osborne, J.N. Perry, P. Rothery, D.B. Roy, R.J. Scott, I.P. Woiwod, C. Birchall, M.P. Skellern, J.H. Walker, P. Baker, E.L. Browne, A.J. Dewar, B.H. Garner, L.A. Haylock, S.L. Horne, N.S. Mason, R.J. Sands, and M.J. Walker. 2003. Invertebrate responses to the management of genetically modified herbicide-tolerant and conventional spring crops. II. Within field epigeal and aerial arthropods. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences* 358(1439):863–1877.
- Hawes, C., A.J. Haughton, J.L. Osborne, D.B. Roy, S.J. Clark, and J.N. Perry. 2003. Responses of plants and invertebrate trophic groups to contrasting herbicide regimes in the farm scale evaluations of genetically modified herbicide-tolerant crops. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences* 358(1439):1899–1913.

- Hayami, Y., and V.W. Ruttan. 1985. *Agricultural Development: An International Perspective*. 2nd edition. Baltimore: Johns Hopkins University Press.
- Hayata, Y., Y. Niimi, and N. Iwasaki. 1995. Inducing parthenocarpic fruit of watermelon with plant bioregulators. *Acta Horticulturae* (394):235–240.
- Headings, M.E. 2000. Biology and behavior of the small hive beetle, *Aethina tumida*, a new potential pest in the Western Hemisphere. Pp. 227–232 in *Proceedings of the 35th Annual Meeting, Caribbean Food Crops Society, Castries, St-Lucia, July 25–31, 1999*, W. Colon, ed. Isabela, Puerto Rico: Caribbean Food Crops Society.
- Heal, G. M. 2000. *Nature and the Marketplace: Capturing the Value of Ecosystem Services*. Washington: Island Press.
- Heard, M.S., C. Hawes, G.T. Champion, S.J. Clark, L.G. Firbank, A.J. Haughton, A.M. Parish, J.N. Perry, P. Rothery, R.J. Scott, M.P. Skellern, G.R. Squire, and M.O. Hill. 2003. Weeds in fields with contrasting conventional and genetically modified herbicide-tolerant crops: effects on abundance and diversity. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences* 358(1439):1819–1832.
- Hedrick, P.W., J. Gadau, and R.E. Page, Jr. 2006. Genetic sex determination and extinction. *Trends in Ecology and Evolution* 21:55–57.
- Heinrich, B. 1979. *Bumblebee Economics*. Cambridge, Mass.: Harvard University Press.
- Heinrich, B. 2004. *Bumblebee Economics*. Revised edition. Cambridge, Mass.: Harvard University Press.
- Heinz, C. 2005. Honey Bees and RIFA Seminar. Almond Board of California. Available at: <http://almondboard.files.cms-plus.com/PDFs/Heintz%20-%20ABC%20Research%20Review.pdf>. Accessed December 28, 2005.
- Heiser, C.B. 1954. Variation and subspeciation in the common sunflower, *Helianthus annuus*. *American Midland Naturalist* 51:287–305.
- Heithaus, E.R. 1982. Coevolution between bats and plants. Pp. 327–367 in *Ecology of Bats*, T.H. Kunz, ed. New York: Plenum Press.
- Hellmich, R.L. 1986. Mating European honey-bee queens to European drones in areas with Africanized bees. *American Bee Journal* 126(12):830–831.
- Hellmich, R.L. 1991. Continuing commercial queen production after the arrival of Africanized honey bees. Pp. 187–197 in *The “African” Honey-Bee*. Oxford: Westview Press.
- Hellmich, R.L., A.M. Collins, R.G. Danka, and T.E. Rinderer. 1988. Influencing matings of European honey bee queens in areas with Africanized honey bees (Hymenoptera: Apidae). *Journal of Economic Entomology* 81(3):796–799.
- Hellmich, R.L., B.D. Siegfried, M.K. Sears, D.E. Stanley-Horn, M.J. Daniels, H.R. Mattila, T. Spencer, K.G. Bidne, and L.C. Lewis. 2001. Monarch larvae sensitivity to *Bacillus thuringiensis*-purified proteins and pollen. *Proceedings of the National Academy of Sciences USA* 98:11925–11930.
- Helson, B.V., K.N. Barber, and P.D. Kingsbury. 1994. Laboratory toxicology of six forestry insecticides to four species of bee (Hymenoptera: Apoidea). *Archives of Environmental Contamination and Toxicology* 27:107–114.
- Herrera, C.M. 1987. Components of pollinator “quality”: comparative analysis of a diverse insect assemblage. *Oikos* 50:79–90.
- Herrera, C.M. 1989. Seed dispersal by animals: a role in angiosperm diversification? *American Naturalist* 133:309–322.
- Herrera, C.M. 2000. Flower-to-seedling consequences of different pollination regimes in an insect-pollinated shrub. *Ecology* 81:15–29.
- Herring, T. 2003. The yellow pond lily of the Ozarks (*Nuphar ozarkana*): a pollination ecology study. Thesis presented to the faculty of the Graduate School of Saint Louis University in partial fulfillment of the requirements for the degree of Masters of Sciences.
- Hickman, J.C. 1974. Pollination by ants: a low-energy system. *Science* 184(4143):1290–1292.

- Hill, J.K., C.D. Thomas, and B. Huntley. 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society of London* 266:1197–1206.
- Hillesheim, E., W. Ritter, and D. Bassand. 1996. First data on resistance mechanisms of *Varroa jacobsoni* (Oud.) against tau-fluvalinate. *Experimental and Applied Acarology* 20(5):283–296.
- Hines, H.M., and S.D. Hendrix. 2005. Bumble bee (Hymenoptera: Apidae) diversity and abundance in tallgrass prairie patches: effects of local and landscape floral resources. *Environmental Entomology* 34:1477–1484.
- Hingston, A.B., and P.B. McQuillan. 1997. Displacement of Tasmanian native megachilid bees by the recently introduced bumblebee *Bombus terrestris* (Linnaeus 1758)(Hymenoptera: Apidae). *Australian Journal of Zoology* 47:59–65.
- Hingston, A.B., and P.B. McQuillan. 1998. Does the recently introduced bumblebee *Bombus terrestris* (Apidae) threaten Australian ecosystems? *Australian Journal of Ecology* 23:539–549.
- Hirsch, M., S. Pfaff, and V. Wolters. 2003. The influence of matrix type on flower visitors of *Centaurea jacea* L. *Agriculture Ecosystems and Environment* 98:331–337.
- Hitchcock, J.D., J.O. Moffett, J.J. Lockett, and J.R. Elliott. 1970. Tylosin for control of American foulbrood disease in honey bees [*Bacillus larvae*, *Apis mellifera*]. *Journal of Economic Entomology* 63(1):204–207.
- Hoebcke, E.R., and A.G.J. Wheeler. 1999. *Anthidium oblangatum* (Illiger): an Old World bee (Hymenoptera: Megachilidae) new to North America, and new North American records for another adventive species, *A. manicatum* (L.). *Scientific Papers, Natural History Museum, The University of Kansas—a continuation of the University of Kansas Science Bulletin* 24:21–24.
- Hoff, F.L., and J.K. Phillips. 1989. Honey: Background for 1990 farm legislation. *AGES* 89–43.
- Hölldobler, B., and E.O. Wilson. 1990. *The Ants*. Cambridge, Mass.: Belknap Press.
- Hölldobler, B., and E.O. Wilson. 1994. *Journey to the Ants: A Story of Scientific Exploration*. Cambridge, Mass.: Belknap Press.
- The Honeybee Genome Sequencing Consortium. 2006. Insights into social insects from the genome of the honeybee *Apis mellifera*. *Nature* 443:931–949.
- Hood, W.M. 2004a. The small hive beetle, *Aethina tumida*: a review. *Bee World* 85:51–59.
- Hood, W.M. 2004b. The biology and management of small hive beetles. In *Proceedings of the 8th IBRA International Conference on Tropical Bees and VI Encontro sobre Abelhas, Ribeirao Preto, Brasil, September 6–10, 2004*. K.H. Hartfelder, D. de Jong, R.A. Pereira, A. dos Santos Cristino, M.M. Morais, E.D. Tanaka, A.P. Lourenco, J.E.B. da Silva, G.F. de Almeida, and A.M. de Nascimento, eds. Cardiff: International Bee Research Association.
- Hoopingarner, R. 1991. Assessment of the declining feral honeybee population. *Annual Report Indiana State Horticultural Society. The Society* 121:154–157.
- Hoopingarner, R.H., and G.D. Waller. 1992. Crop pollination. Pp. 1043–1082 in *The Hive and the Honey Bee*, J.M. Graham, ed. Hamilton, Ill.: Dadant and Sons.
- Hoppe, H., W. Ritter, and E.W.C. Stephen. 1989. The control of parasitic bee mites: *Varroa jacobsoni*, *Acarapis woodi* and *Tropilaelaps clareae* with formic acid. *American Bee Journal* 129:739–742.
- Hughes, M.J. 1996. Commercial rearing of bumble bees. Pp. 40–47 in *Bumble Bees for Pleasure and Profit*, A. Matheson, ed. Cardiff: International Beekeeper Research Association.
- Hunt, G.J., E. Guzman-Novoa, M.K. Fondrk, and R.E. Page, Jr. 1998. Quantitative trait loci for honey bee stinging behavior and body size. *Genetics* 148(3):1203–1213.
- Hunter, L.A., J.A. Jackman, and E.A. Sugden. 1993. Detection records of Africanized honey bees in Texas during 1990, 1991 and 1992. *Southwestern Entomologist* 18(2):79–89.

- Husband, R.W., and R.N. Sinha. 1970. A revision of the genus *Locustacarus* with a key to the genera of the family Podapolipidae (Acarina). *Annals of the Entomological Society of America* 63(4):1152–1162.
- Hutson, A.M., S.P. Mickleburgh, and P.A. Racey, compilers. 2001. *Microchiropteran Bats: Global Status Survey and Conservation Action Plan*. IUCN/SSC Chiroptera Specialist Group. Gland, Switzerland and Cambridge: IUCN. 258 pp.
- Huxley, C.R., and D.F. Cutler, eds. 1991. *Ant-Plant Interactions*. New York: Oxford University Press.
- Imhoof, B., and P. Schmid-Hempel. 1999. Colony success of the bumble bee, *Bombus terrestris*, in relation to infections by two protozoan parasites, *Crithidia bombi* and *Nosema bombi*. *Insectes Sociaux* 46:233–238.
- Imms, A.D. 1921. Isle of Wight disease in hive bees. *Nature* 2687:283–284.
- Inouye, D.W. 1977. Species structure of bumblebee communities in North America and Europe. Pp. 35–40 in W. J. Mattson, ed., *The Role of Arthropods in Forest Ecosystems*. New York: Springer Verlag.
- Intenthron, M., and J. Gerrard. 1999. *Making Nests for Bumble Bees*. Cardiff: International Beekeeper Research Association. 38 pp.
- IUCN (International Union for the Conservation of Nature and Natural Resources/The World Conservation Union). 1996. 1996 IUCN Red List of Threatened Animals. Available at: <http://www.iucn.org/themes/ssc/96anrl/intro.htm>. Accessed March 31, 2006.
- Jacobs, G.H. 1992. Ultraviolet vision in vertebrates. *American Zoologist* 32:544–554.
- Janson, C.H., J. Terborgh, and L.H. Emmons. 1981. Non-flying mammals as pollinating agents in the Amazonian forest. *Biotropica* 13:1–6 Suppl. S.
- Janzen, D.H. 1974. The deflowering of Central America. *Natural History* 83:48–53.
- Janzen, D.H. 1985. The natural history of mutualisms. Pp. 40–99 in *The Biology of Mutualism*, D.H. Boucher, ed. New York: Oxford University Press.
- Janzen, D.H. 2004. Setting up tropical biodiversity for conservation through non-damaging use: participation by parataxonomists. *Journal of Applied Ecology* 41:181–187.
- Jarlan A., D. de Oliveira, and J. Gingras. 1997. Effects of *Eristalis tenax* (Diptera: Syrphidae) pollination on characteristics of greenhouse sweet pepper fruits. *Journal of Economic Entomology* 90(6):1650–1654.
- Javorek, S.K., K.E. Mackenzie, and S.P. Vander-Kloet. 2002. Comparative pollination effectiveness among bees (Hymenoptera: Apoidea) on lowbush blueberry (Ericaceae: *Vaccinium angustifolium*). *Annals of the Entomological Society of America* 95(3):345–351.
- Jaycox, E.R. 1967. An adventive *Anthidium* in New York State (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 40:124–126.
- Jennersten, O. 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. *Conservation Biology* 2:359–367.
- Jesse, L.C.H., and J.J. Obrycki. 2002. Assessment of the non-target effects of transgenic *Bt* corn pollen and anthers on the milkweed tiger moth, *Euchatias egle* Drury (Lepidoptera: Arctiidae). *Journal of the Kansas Entomological Society* 75:55–58.
- Jimenez-Hidalgo I., G. Virgen, D. Martinez, G. Vandemark, J. Alego, and V. Olalde. 2004. Identification and characterization of soft rot bacteria of *Agave tequilana* Weber Var Azul. *Journal of Plant Pathology* 110:317–331.
- Johansen, C.A. 1977. Pesticides and pollinators. *Annual Review of Entomology* 22:177–192.
- Johansen, C.A., and D.F. Mayer. 1990. *Pollinator Protection. A Bee and Pesticide Handbook*. Cheshire, Conn.: Wicwas Press.
- Johnson, S.D., C.L. Collin, H.J. Wissman, E. Halvarsson, and J. Agren. 2004. Factors contributing to variation in seed production among remnant populations of the endangered daisy *Gerbera aurantiaca*. *Biotropica* 36(2):48–155.
- Jones, F.M., and C.P. Kimball. 1943. The Lepidoptera of Nantucket and Martha's Vineyard. *Nantucket Maria Mitchell Association* 4:1–217.

- Jones, R., and P. Munn. 1998. *Habitat Management for Wild Bees and Wasps*. Cardiff: International Beekeeper Research Association. 38 pp.
- Jousselin, E., J.Y. Rasplus, and F. Kjellberg. 2001. Shift to mutualism in parasitic lineages of the fig/fig wasp interaction. *Oikos* 94:287–294.
- Juenger, T., and J. Bergelson. 2000. The evolution of compensation to herbivory in scarlet gilia, *Ipomopsis aggregata*; herbivore-imposed selection and the quantitative genetics of tolerance traits. *Evolution* 54(3):764–777.
- Kandori, I. 2002. Diverse visitors with various pollinator importance and temporal change in the important pollinators of *Geranium thunbergii* (Geraniaceae). *Ecological Research* 17(3):283–294.
- Kanga, L.H.B., W.A. Jones, and R.R. James. 2003a. Field trials using the fungal pathogen, *Metarhizium anisopliae* (Deuteromycetes: Hyphomycetes) to control the ectoparasitic mite, *Varroa destructor* (Acari: Varroidae) in honey bee, *Apis mellifera* (Hymenoptera: Apidae) colonies. *Journal of Economic Entomology* 96:1091–1099.
- Kanga, L.H.B., R.R. James, and D.G. Boucias. 2003b. *Hirsutella thompsonii* and *Metarhizium anisopliae* as potential microbial control agents of *Varroa destructor*, a honey bee parasite. *Journal of Invertebrate Pathology* 81:175–184.
- Kato, M. 2000. Anthophilous insect community and plant-pollinator interactions on Amami Islands in the Ryukyu Archipelago, Japan. *Contributions from the Biological Laboratory, Kyoto University* 29:157–252.
- Kato, M., A. Shibata, T. Yasui, and H. Nagamasu. 1999. Impact of introduced honeybees, *Apis mellifera*, upon native bee communities in the Bonin (Ogasawara) Islands. *Researches on Population Ecology* 41:217–228.
- Kays, R.W. 1999. Food preferences of kinkajous (*Potos flavus*): a frugivorous carnivore. *Journal of Mammalogy* 80:589–599.
- Kearns, C.A. 1990. The role of fly pollination in montane habitats. Dissertation. University of Maryland, College Park.
- Kearns, C.A., and D.W. Inouye. 1993. *Techniques for Pollination Biologists*. Niwot, Colo.: University Press of Colorado.
- Kearns, C.A., and D.W. Inouye. 1997. Pollinators, flowering plants, and conservation biology. *BioScience* 47:297–307.
- Kearns, C., and J. Thomson. 2001. *The Natural History of Bumble Bees. A Sourcebook for Investigations*. Boulder: University Press of Colorado.
- Kearns, C.A., D.W. Inouye, and N.M. Waser. 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics* 29:83–112.
- Kemp, W.P. 2000. The future of crop pollination. *American Bee Journal* 140:851–853.
- Kephart, D. 2005. Pollen-pollinator limitation. Pp. 364–370 in *Practical Pollination Biology*, A. Dafni, P.G. Kevan, and B.C. Husband, eds. Cambridge, Canada: Enviroquest.
- Kephart, S., and K. Theiss. 2003. Pollinator-mediated isolation in sympatric milkweeds (*Asclepias*): do floral morphology and insect behavior influence species boundaries? *New Phytologist* 161:265–277.
- Kevan, P.G. 1972. Insect pollination of high arctic flowers. *Journal of Ecology* 60:813–847.
- Kevan, P.G. 1974. Pollination, pesticides and environmental quality. *BioScience* 24:198–199.
- Kevan, P.G. 1975a. Pollination and environmental conservation. *Environmental Conservation* 2:222–227.
- Kevan, P.G. 1975b. Forest application of the insecticide fenitrothion and its effects on wild bee pollinators (Hymenoptera: Apoidea) of lowbush blueberries (*Vaccinium* spp.) in southern New Brunswick, Canada. *Biological Conservation* 7:301–309.
- Kevan, P.G. 1984. Pollination by animals and angiosperm biosystematics. Pp. 271–292 in *Plant Biosystematics*, W.F. Grant, ed. Toronto: Academic Press.
- Kevan, P.G. 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. *Agriculture, Ecosystems and Environment* 74:373–393.

- Kevan, P.G. 2001. Pollination: plinth, pedestal, and pillar for terrestrial productivity. The why, how, and where of pollination protection, conservation, and promotion. Pp. 7–68 in *Bees and Crop Pollination—Crisis, Crossroads, Conservation*, C.S. Stubbs and F.A. Drummond, eds. Proceedings, Entomological Society of America. Lanham, Md.: Thomas Say Publications in Entomology.
- Kevan, P.G., and D. Eisikowitch. 1990. Self- and cross-pollination in canola (*Brassica napus* L. var. O.A.C. Triton) and its implication on seed germination. *Euphytica* 45:39–41.
- Kevan, P.G., and V.L. Imperatriz-Fonseca, eds. 2002. *Pollinating Bees: The Conservation Link Between Agriculture and Nature*. Proceedings of the Workshop on the Conservation and Sustainable Use of Pollinators in Agriculture, with Emphasis on Bees, held in S. Paulo, Brazil in October 1998. Brazil: Ministry of Environment. 313 pp.
- Kevan, P.G., and D.M. Kendall. 1997. Liquid assets for fat bankers: summer nectarivory by migratory moths in the Rocky Mountains, Colorado, USA. *Arctic and Alpine Research* 29:478–482.
- Kevan, P.G., and T.P. Phillips. 2001. The economic impacts of pollinator declines: an approach to assessing the consequences. *Conservation Ecology* 5(1):8.
- Kevan, P.G., and R.C. Plowright. 1995. Impact of pesticides on forest pollination. Pp. 607–618 in *Forest Insect Pests in Canada*, J.A. Armstrong and W.G.H. Ives, eds. Ottawa: Natural Resources Canada.
- Kevan, P.G., E.A. Clark, and V.G. Thomas. 1990. Insect pollinators and sustainable agriculture. *American Journal of Alternative Agriculture* 5:13–22.
- Kevan, P.G., W.A. Straver, M. Offer, and T.M. Laverty. 1991. Pollination of greenhouse tomatoes by bumblebees in Ontario. *Proceedings of the Entomological Society of Ontario* 122:15–19.
- Kevan, P.G., C.F. Greco, and S. Belaoussoff. 1997. Log-normality of biodiversity and abundance in diagnosis and measuring of ecosystemic health: pesticide stress on pollinators on blueberry heaths. *Journal of Applied Ecology* 34:1122–1136.
- Kevan, P.G., V.L. Shipp, J.P. Kapongo, and M.S. Al-mazra'awi. 2005. Bee pollinators vector biological control agents against insect pests of horticultural crops. Pp. 77–95 in *First Short Course on Pollination of Horticulture Plants*, J.M. Guerra-Sanz, A. Roldán Serrano, and A. Mena Granero, eds. La Mojonera, Spain: CIFA.
- Kevan, P.G., M.A. Hannan, N. Ostiguy, and E. Guzman-Novoa. 2006. A summary of the *Varroa*-virus disease complex in honey bees. *American Bee Journal* 146:694–697.
- Kim, J., N. Williams, and C. Kremen. 2006. Effects of cultivation and proximity to natural habitat on ground-nesting native bees in California sunflower fields. *Journal of the Kansas Entomological Society* 79(4):309–320.
- Kincaid. 1963. The ant-plant, *Orthocarpus pusillus*, Bentham (Scrophulariaceae). *Transactions of the American Microscopical Society* 82:101–105.
- Kingsley, K.J. 1996. Behavior of the Delhi Sands flower-loving fly (Diptera: Mydidae), a little-known endangered species. *Annals of the Entomological Society of America* 89:883–891.
- Kirk, W.D.J. 1984. Pollen-feeding in thrips (Insecta: Thysanoptera). *Journal of Zoology* 204:107–117.
- Kirk, W.D.J. 1985. Pollen-feeding and the host specificity and fecundity of flower thrips (Thysanoptera). *Ecological Entomology* 10:281–289.
- Kirk, W.D.J. 1988. Thrips and pollination biology. Pp. 129–135 (Chapter 10) in *Dynamics of Insect-Plant Interaction*, T.N. Ananthkrishnan and A. Raman, eds. New Delhi: Oxford and IBH.
- Kirk, W.D.J. 1993. Thrips and pollen. Pp. 251–258 (Chapter 15) in *Advances in Thysanopterology*, J.S. Bhatti, ed. New Delhi: Scientia Publishing.
- Kirk, W.D.J. 1997. Feeding. Pp. 119–174 (Chapter 4) in *Thrips as Crop Pests*, T. Lewis, ed. Wallingford: CAB International.

- Klanderud, K., and H.J.B. Birks. 2003. Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *The Holocene* 13:1–6.
- Kleijn, D., F. Berendse, R. Smit, and N. Gilissen. 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature* 413:723–725.
- Kleijn, D., F. Berendse, R. Smit, N. Gilissen, J. Smit, B. Brak, and R. Groeneveld. 2004. The ecological effectiveness of agri-environment schemes in different agricultural landscapes in The Netherlands. *Conservation Biology* 18:775–786.
- Kleijn, D., R.A. Baquero, Y. Clough, M. Díaz, J. De Esteban, F. Fernández, D. Gabriel, F. Herzog, A. Holzschuh, R. Jöhl, E. Knop, A. Kruess, E.J.P. Marshall, I. Steffan-Dewenter, T. Tscharntke, J. Verhulst, T.M. West, and J.L. Yela. 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters* 9(3):243.
- Klein, A.M., I. Steffan-Dewenter, D. Buchori, and T. Tscharntke. 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conservation Biology* 16:1003–1014.
- Klein, A.M., I. Steffan-Dewenter, and T. Tscharntke. 2003a. Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society of London Series B—Biological Sciences* 270:955–961.
- Klein, A.M., I. Steffan-Dewenter, and T. Tscharntke. 2003b. Bee pollination and fruit set of *Coffea arabica* and *C-canephora* (*Rubiaceae*). *American Journal of Botany* 90:153–157.
- Klein, A.M., I. Steffan-Dewenter, and T. Tscharntke. 2003c. Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *Journal of Applied Ecology* 40:837–845.
- Klein, A.M., B.E. Vaissière, J.H. Cane, I. Steffan-Dewenter, S.A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London Series B*. 274:303–313.
- Knight, T.M., J.A. Steets, J.C. Vamasi, S.J. Mazer, M. Burd, D.R. Campbell, M.R. Dudash, M.O. Johnston, R.J. Mitchell, and T. Ashman. 2005a. Pollen limitation of plant reproduction: pattern and process. *Annual Review of Ecology Evolution and Systematics* 36:467–497.
- Knight, T.M., M.W. McCoy, J.M. Chase, K.A. McCoy, and R.D. Holt. 2005b. Trophic cascades across ecosystems. *Nature* 437:880–883.
- Knight, T.M., J.A. Steets, and T.-L. Ashman. 2006. A quantitative synthesis of pollen supplementation experiments highlights the contribution of resource reallocation to estimates of pollen limitation. *American Journal of Botany* 92:2702–2776.
- Knop, E., D. Kleijn, F. Herzog, and B. Schmid. 2006. Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. *Journal of Applied Ecology* 43:120–127.
- Knudsen J.T., L. Tollsten, and L.G. Bergstrom. 1993. Floral scents—A checklist of volatile compounds isolated by head-space techniques. *Phytochemistry* 33:253–280.
- Knudsen, J.T., L. Tollsten, I. Groth, G. Bergstrom, and R.A. Raguso. 2004. Trends in floral scent chemistry in pollination syndromes: floral scent composition in hummingbird-pollinated taxa. *Botanical Journal of the Linnean Society* 146:191–199.
- Knuth, P. 1906. *Handbook of Flower Pollination*. Volume I. Translated by J.R. Ainsworth Davis, Oxford: Clarendon Press. 382 pp.
- Knuth, P. 1908. *Handbook of Flower Pollination*. Volume II. Translated by J.R. Ainsworth Davis, Oxford: Clarendon Press. 705 pp.
- Knuth, P. 1912. *Handbook of Flower Pollination*. Volume II. Translated by J.R. Ainsworth Davis, Oxford: Clarendon Press.
- Koehler, S.D., and E.H. Williams. 2000. The diversity and abundance of North American butterflies vary with habitat disturbance and geography. *Journal of Biogeography* 27(4):785–794.
- Koeniger, N., G. Koeniger, and M. Delfinado-Baker. 1983. Observations on mites of the Asian honeybee species. *Apidologie* 14:1978–204.

- Kogan, M. 1998. Integrated pest management: historical perspectives and contemporary developments. *Annual Review of Entomology* 43:243–270.
- Kölreuter, J.G. 1761. Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen. Leipzig.
- Koltunow, A.M., A. Vivian-Smith, and S.R. Sykes. 2000. Molecular and conventional breeding strategies for seedless citrus. *Acta Horticulturae (ISHS)* 535:169–174.
- Kovach, J., R. Petzoldt, and G.E. Harman. 2000. Use of honeybees and bumble bees to disseminate *Trichoderma harzianum* 1295-22 to strawberries for *Botrytis* control. *Biological Control* 18:235–242.
- Kral, R. 1960. A revision of *Asimina* and *Deeringothamus* (Annonaceae). *Brittonia* 12:233–278.
- Kraus, B., and R.E. Page. 1995. Effect of *Varroa jacobsoni* (Mesostigmata: Varroidae) on feral *Apis mellifera* (Hymenoptera: Apidae) in California. *Environmental Entomology* 24:66, 1473–1480.
- Krebbs, K., R.A. Medellin, Y. Petryzsyn, A. McIntire, L. Lewis, and D. Dalton. 2005. Lesser long-nosed bat. Sonorensis. Newsletter of the Arizona-Sonora Desert Museum, Tucson, Winter 2005 issue.
- Krebs, C.J. 1999. *Ecological Methodology*. Menlo Park: Addison Wesley Longman.
- Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* 2:203–217.
- Kremen, C., and R. Chaplin. Forthcoming (in press). Insects as providers of ecosystem services. In *Insect Conservation Biology: Proceedings of the Royal Entomological Society's 23rd Symposium*, A.J.A. Stewart, T.R. New, and O.T. Lewis, eds. Wallingford: CABI Publishing.
- Kremen, C., and R.S. Ostfeld. 2005. A call to ecologists: measuring, analyzing, and managing ecosystem services. *Frontiers in Ecology and the Environment* 3:540–548.
- Kremen, C., and T. Ricketts. 2000. Global perspectives on pollination disruptions. *Conservation Biology* 14:1226–1228.
- Kremen, C., R.K. Colwell, T.L. Erwin, D.D. Murphy, R.F. Noss, and M.A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* 7:796–808.
- Kremen, C., R.L. Bugg, N. Nicola, S.A. Smith, R.W. Thorp, and N.M. Williams. 2002a. Native bees, native plants and crop pollination in California. *Fremontia* 30:41–49.
- Kremen, C., N.M. Williams, and R.W. Thorp. 2002b. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences USA* 99:16812–16816.
- Kremen, C., N.M. Williams, R.L. Bugg, J.P. Fay, and R.W. Thorp. 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecology Letters* 7:1109–1119.
- Krombein, K.V. 1967. *Trap-Nesting Wasps and Bees: Life Histories, Nests, and Associates*. Washington: Smithsonian Press. 570 pp.
- Kron, P., B.C. Husband, and P.G. Kevan. 2001a. Across- and along-row pollen dispersal in high density apple orchards: insights from allozyme markers. *Journal of Horticultural Science and Biotechnology* 76:286–294.
- Kron, P., B.C. Husband, P.G. Kevan, and S. Belaussoff. 2001b. Phenology, pollination neighborhood and distance affect pollen dispersal in high density apple orchards. *HortScience* 36:1039–1046.
- Kudo, G., Y. Nishikawa, T. Kasagi, and S. Kosuge. 2004. Does seed production of spring ephemerals decrease when spring comes early? *Ecological Research* 19(2):255–259.
- Kukuk, P. 1989. Evolutionary genetics of a primitive eusocial halictine bee, *Dialictus zephyrus*. Pp. 183–202 in *The Genetics of Social Evolution*, M.D. Breed and R.E. Page, eds. Boulder: Westview.

- Kunin, W.E. 1997. Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. *Journal of Ecology* 85:225–234.
- Kunz, T.H. 1982. Roosting ecology of bats. Pp. 1–55 in *Ecology of Bats*, T.H. Kunz, ed. New York: Plenum Press.
- Labandeira, C.C. 1998. How old is the flower and the fly? *Science* 280:85–88.
- Labandeira, C.C., D.L. Dilcher, D.R. Davis, and D.L. Wagner. 1994. Ninety-seven million years of angiosperm-insect association: paleobiological insights into the meaning of coevolution. *Proceedings of the National Academy of Sciences USA* 91:12278–12282.
- Ladley, J.J., and D. Kelly. 1995. Explosive New Zealand mistletoe. *Nature* 378:766.
- Laidlaw, H.H., Jr. 1977. *Instrumental Insemination of Honey Bee Queens*. Hamilton, Ill.: Dandant.
- Laidlaw, H.H., Jr. 1992. Production of queens and package bees. Pp. 989–1042 in *The Hive and the Honey Bee*. Hamilton, Ill.: Dadant and Sons.
- Laidlaw, H.H., Jr., and R.E. Page, Jr. 1998. *Queen Rearing and Bee Breeding*. Cheshire, Conn.: WicWas Press. 224 pp.
- Lake, J.C., and L. Hughes. 1999. Nectar production and floral characteristics of *Tropeolum majus* L. grown in ambient and elevated carbon dioxide. *Annals of Botany* 84:535–541.
- Lammers, T.G., S.G. Weller, and A.K. Sakai. 1987. Japanese White-eye, an introduced passerine, visits the flowers of *Clermontia arborescens*, an endemic Hawaiian Lobelioid. *Pacific Science* 41:74–77.
- Lamont, B.B., P.G.L. Klinkhamer, and E.T.F. Witkowski. 1993. Population fragmentation may reduce fertility to zero in *Banksia goodii*—a demonstration of the Allee effect. *Oecologia* 94:446–450.
- Langstroth, L.L. 1862. *The Hive and the Honey Bee*. New York: C.M. Saxton.
- Lapidge, K.L., B.P. Oldroyd, and M. Spivak. 2002. Seven suggestive quantitative trait loci influence hygienic behavior of honey bees. *Naturwissenschaften* 89(12):565–568.
- Larrea-Reynoso, E. 1998. Estudios preliminares para el control de los hongos *Fusarium*, *Verticillium*, *Asterina* y de una bacteria no clasificada en agave azul (*Agave tequilana* Weber var. azul). *Revista Mexicana de Fitopatología* 16:125.
- Larsen, T.H., N. Williams, and C. Kremen. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters* 8:538–547.
- Larson, B.M.H., and S.C.H. Barrett. 2000. A comparative analysis of pollen limitation in flowering plants. *Biological Journal of the Linnean Society* 69:503–520.
- Larson, D.L., P.J. Anderson, and W. Newton. 2001. Alien plant invasion in mixed-grass prairie: effects of vegetation type and anthropogenic disturbance. *Ecological Applications* 11(1):128–141.
- Law, B.S., and M. Lean. 1999. Common blossom bats (*Syconycteris australis*) as pollinators in fragmented Australian tropical rainforest. *Biological Conservation* 91:201–212.
- Leclercq, J., C. Gaspar, J.-L. Marchal, C. Verstraeten, and C. Wonville. 1980. Analyse des 1600 premières cartes de l'Atlas provisoire des Insectes de Belgique, et première liste rouge d'Insectes menacés dans la faune belge. *Notes fauniques de Gembloux* 4:1–104.
- Lepczyk, C.A. 2005. Integrating published data and citizen science to describe bird diversity across a landscape. *Journal of Applied Ecology* 42:672–677.
- Lepczyk, C.A., A.G. Mertig, and J. Liu. 2004. Landowners and cat predation across rural-to-urban landscapes. *Biological Conservation* 115:191–201.
- Lepers, E., E.F. Lambin, A.C. Janetos, R. DeFries, F. Achard, N. Ramankutty, and R.J. Scholes. 2005. A synthesis of information on rapid land-cover change for the period 1981–2000. *Bioscience* 55:115–124.

- Lesica, P., and B. McCune. 2004. Decline of arctic-alpine plants at the southern margin of their range following a decade of climatic warming. *Journal of Vegetation Science* 15:679–690.
- Levin, M.D. 1983. Value of bee pollination to U.S. agriculture. *Bulletin of the Entomological Society of America* 29:59–51.
- Lewis, T. 1973. *Thrips: Their Biology, Ecology and Economic Importance*. London and New York: Academic Press.
- Lewis, T., ed. 1997. *Thrips as Crop Pests*. New York: CAB International.
- Li, W., K. Wu, X. Wang, G. Wang, and Y. Guo. 2005. Impact of pollen grains from *Bt* Transgenic corn on the growth and development of Chinese Tussah silkworm, *Antheraea pernyi* (Lepidoptera: Saturniidae). *Environmental Entomology* 34(4):922–928(7).
- Lilleboe, D. 2000. California's Sacramento Valley. *Sunflower Magazine* February. Available at: <http://www.sunflowerusa.com/magazine/details.asp?ID=160&Cat=6>. Accessed July 14, 2006.
- Lin, S., and G. Bernardello. 1999. Flower structure and reproductive biology in *Aspidosperma quebracho-blanco* (Apocynaceae), a tree pollinated by deceit. *International Journal of Plant Sciences* 160:869–878.
- Linsley, E.G. 1958. The ecology of solitary bees. *Hilgardia* 27:543–599.
- Lippok, B., and S.S. Renner. 1997. Pollination of *Nuphar* (Nymphaeaceae) in Europe: flies and bees rather than *Donacia* beetles. *Plant Systematics and Evolution* 207:273–283.
- Little, K.J., G. Dieringer, and M. Romano. 2005. Pollination ecology, genetic diversity and selection on nectar spur length in *Platanthera lacera* (Orchidaceae). *Plant Species Biology* 20:183–190.
- Liu, T.P., and M.E. Nasr. 1993. Preventive treatment of tracheal mites, *Acarapis woodi* (Rennie) with vegetable oil extender patties in the honey bee, *Apis mellifera* L. colonies. *American Bee Journal* 133:873–875.
- Lodesani, M., and M. Costa. 2005. Limits of chemotherapy in beekeeping: development of resistance and the problem of residues. *Bee World* 86(4):102–109.
- Loper, G.M. 1995. A documented loss of feral bees due to mite infestations in S. Arizona. *American Bee Journal* 135:823–824.
- Loper, G.M. 1996. Feral colonies and tracheal mites. *Bee Culture* 124:27.
- Loper, G.M. 1997. Over-winter losses of feral honey bee colonies in southern Arizona, 1992–1997. *American Bee Journal* December:823.
- Loper, G.M., D. Sammataro, J. Finley, and J. Cole. 2006. Feral honey bees in Southern Arizona, 10 years after *Varroa* infestation. *American Bee Journal* 146:521–524.
- Losey, J.E., and M. Vaughan. 2006. The economic value of ecological services provided by insects. *Bioscience* 56:311–323.
- Losey, J.E., L.S. Rayor, and M.E. Carter. 1999. Transgenic pollen harms monarch larvae. *Nature* 399:214.
- Lumkin, D. 2005. Knuckling it through a winter with *Varroa*. *Bee Culture* 133:22–24.
- Lundie, A.E. 1940. The Small Hive Beetle, *Aethina tumida*. *Science Bulletin* 220. Union of South Africa: Department of Agriculture and Forestry. 30 pp.
- MacArthur, R.H., and E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton: Princeton University Press.
- MacDonald, O.C., I. Meakin, and D.M. Richardson. 2003. The role and impact of the regulator in resistance management. Pp. 703–708 in the BCPC International Congress: Crop Science and Technology, Volumes 1 and 2. Proceedings of an International Congress held at the SECC, Glasgow, Scotland, UK, November 10–12, 2003.
- Macedo, P.A., M.D. Ellis, and B.D. Siegfried. 2002. Detection and quantification of fluralinate resistance in *Varroa* mites in Nebraska. *American Bee Journal* 142:523–526.
- Macfarlane, R.P., K.D. Patten, L.A. Royce, B.K.W. Wyatt, and D.F. Mayer. 1994. Management potential of sixteen North American bumble bee species. *Melandria* 50:1–12.

- Macfarlane, R.P., J.J. Lipa, and H.J. Liu. 1995. Bumble bee pathogens and internal enemies. *Bee World* 76:130–148.
- Machado, C.A., E.A. Herre, S. McCafferty, and E. Bermingham. 1996. Molecular phylogenies of fig pollinating and non-pollinating wasps and the implications for the origin and devolution of the fig-fig wasp mutualism. *Journal of Biogeography* 23:531–542.
- Machado, C.A., N. Robbins, M.P.T. Gilbert, and E.A. Herre. 2005. Critical review of host specificity and its coevolutionary implications in the fig/fig-wasp mutualism. *Proceedings of the National Academy of Sciences USA* 102(Suppl 1):6558–6565.
- MacKenzie, K.E. 1997. Pollination requirements of three highbush blueberry (*Vaccinium corymbosum* L.) cultivars. *Journal of the American Society for Horticultural Science* 122(6):891–896.
- MacKenzie, K.E., E. Eickwort, and C. George. 1996. Diversity and abundance of bees (Hymenoptera: Apoidea) foraging on highbush blueberry (*Vaccinium corymbosum* L.) in Central New York. *Journal of the Kansas Entomological Society* 69(4):185–194.
- MacKenzie, K.E., S. Javorek, and K.W. Richards. 1997. The potential of alfalfa leafcutter bees (*Megachile rotundata* L.) as pollinators of cranberry (*Vaccinium macrocarpon* Aiton). *Acta Horticulturae* (437):345–351.
- Mackie, W.W., and F.L. Smith. 1935. Evidence of field hybridization in beans. *American Society of Agronomy Journal* 27:903–909.
- Maeta, Y. 1990. Utilization of wild bees. *Farming Japan* 24(6):13–22.
- Maeta, Y., and T. Kitamura. 1981. Pollinating efficiency of *Osmia cornifrons* in relation to the number of bees required for economic fruit production. *Honeybee Science* 2(2):65–72.
- Maeta, Y., K. Goukon, and T. Tezuka. 1993. Utilization of *Osmia cornifrons* as a pollinator of Japanese pears (Hymenoptera, Megachilidae). *Chugoku Kontyu* (7):1–12.
- Magurran, A.E. 1988. *Ecological Diversity and Its Measurement*. Princeton: Princeton University Press.
- Magurran, A.E. 2004. *Measuring Biological Diversity*. Malden, Mass.: Blackwell Publishers.
- Mainland, D.M., and P. Eck. 1968. Induced parthenocarpic fruit development in highbush blueberry. *Proceedings of the American Society for Horticultural Science* 92:284–289.
- Malloch, J.R. 1918. Occurrence of a European solitary bee (*Andrena wilkella* Kirby) in the eastern United States. *Proceedings of the Biological Society of Washington* 31:61–64.
- Malone, L.A., and M.H. Pham-Delègue. 2001. Effects of transgene products on honey bees (*Apis mellifera*) and bumblebees (*Bombus* sp.). *Apidologie* 32:287–304.
- Mangum, W.A., and R.W. Brooks. 1997. First records of *Megachile* (Callomegachile) *sculpturalis* Smith (Hymenoptera: Megachilidae) in the continental United States. *Journal of the Kansas Entomological Society* 70:140–142.
- Margoluis, R., and N. Salafsky. 1998. *Measures of Success: Designing, Managing, and Monitoring Conservation and Development Projects*. Washington: Island Press.
- Marlin, J.C., and W.E. LaBerge. 2001. The native bee fauna of Carlinville, Illinois, revisited after 75 years: a case for persistence. *Conservation Ecology* 5(1):9.
- Maroto, J.V., A. Miguel, S. Lopez-Galarza, A. San-Bautista, B. Pascual, J. Alagarda, and J.L. Guardiola. 2005. Parthenocarpic fruit set in triploid watermelon induced by CPPU and 2,4-D applications. *Plant Growth Regulation* 45(3):209–213.
- Matheson, A. 1994. *Forage for Bees in an Agricultural Landscape*. Cardiff: International Beekeeper Research Association. 75 pp.
- Matheson, A. 1995. First documented findings of *Varroa jacobsoni* outside its presumed natural range. *Apiacta* 30:1–8.
- Matheson, A., S.L. Buchmann, C. O'Toole, P. Westrich, and I.H. Williams, eds. 1996. *The Conservation of Bees*. London: Academic Press.
- Matsumura, C., J. Yokoyama, and I. Washitani. 2004. Invasion status and potential ecological impacts of an invasive alien bumblebee, *Bombus terrestris* L. (Hymenoptera: Apidae) naturalized in Southern Hokkaido, Japan. *Global Environmental Research* 8:51–66.

- Matton, D.P., N. Nass, A.E. Clarke, and E. Newbigin. 1994. Self-incompatibility: how plants avoid illegitimate offspring. *Proceedings of the National Academy of Sciences USA* 91:1992–1997.
- May, R.M. 1999. How many species? *Philosophical Transactions of the Royal Society—Series B* 330:293–304.
- May, R.M., J.H. Lawton, and N.E. Stork. 1996. Assessing extinction rates. Pp. 1–24 in *Extinction Rates*, J.H. Lawton and R.M. May, eds. Oxford: Oxford University Press.
- Mayer, D.F., and C.A. Johansen. 2003. The rise and decline of *Nomia melanderi* (Hymenoptera: Halictidae) as a commercial pollinator for alfalfa seed. Pp. 139–149 in *For Nonnative Crops, Whence Pollinators of the Future?* K. Strickler and J.H. Cane, eds. *Proceedings, Entomological Society of America*. Lanham, Md.: Thomas Say Publications in Entomology.
- Mayfield, M.M., and G.C. Daily. 2005. Countryside biogeography of neotropical herbaceous and shrubby plants. *Ecological Applications* 15:423–439.
- Mayr, E. 1986. Joseph Gottlieb K reuter’s contributions to biology. *Osiris*, 2nd Series 2:135–176.
- McAlpine, J.F., B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth, and D.M. Wood, coordinators. 1981, 1987, 1989. *Manual of Nearctic Diptera*. Volume 1, Research Branch, Agriculture Canada, Monograph 27, vi + 1–674 pp. [1981], volume 2, Research Branch, Agriculture Canada, Monograph 28, vi + 675–1332 pp. [1987], volume 3, Research Branch, Agriculture Canada, Monograph 32, vi + 1333–1581 pp. [1989].
- McCall, C., and R.B. Primack. 1992. Influence of flower characteristics, weather, time of day, and season on insect visitation rates in three plant communities. *American Journal of Botany* 79:434–442.
- McDade, L.A., and J.A. Weeks. 2004. Nectar in hummingbird-pollinated neotropical plants I: patterns of production and variability in 12 species. *Biotropica* 36:196–215.
- McGraw, J.B., and M.A. Furedi. 2005. Deer browsing and population viability of a forest understory plant. *Science* 307(5711):920–922.
- McGregor, S.E. 1976. *Insect Pollination of Cultivated Crop Plants*. USDA Handbook 496. Washington: U.S. Department of Agriculture, Agricultural Research Service. 411 pp.
- McKay, J.K., C.E. Christian, S. Harrison, and K.J. Rice. 2005. “How local is local?”—a review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology* 13:432–440.
- McKenna, D.D., K.M. McKenna, S.B. Malcolm, and M.R. Berenbaum. 2001. Roadkill Lepidoptera: implications of roadways, roadsides, and traffic rates for the mortality of butterflies in central Illinois. *Journal of the Lepidopterist’s Society* 55(2):63–68.
- McLaughlin, J.F., J.J. Hellmann, C.L. Boggs, and P.R. Ehrlich. 2002. Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences USA* 99:6070–6074.
- Medell n, R.A. 2003. Diversity and conservation of bats in M xico: research priorities, strategies, and actions. *Wildlife Society Bulletin* 31:87–97.
- Medell n, R.A., H.T. Arita, and O. Sanchez. 1997. *Identificaci n de los murci lagos de M xico. Clave de campo*. Asociaci n Mexicana de Mastozoolog a, A.C. Publicaciones Especiales N m. 2. Mexico City.
- Medell n, R.A., J. Guillermo T llez, and J. Arroyo. 2004. Conservation through research and education: an example of collaborative integral actions for migratory bats. Pp. 43–58 in *Conservation of Migratory Pollinators and Their Nectar Corridors in North America*, G. Nabhan, R.C. Brusca, and L. Holter, eds. Arizona–Sonora Desert Museum, *Natural History of the Sonoran Desert Region*, No. 2. Tucson: University of Arizona Press.
- Memmott, J. 1999. The structure of a plant-pollinator food web. *Ecology Letters* 2:276–280.

- Memmott, J., N.M. Waser, and M.V. Price. 2004. Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London Series B—Biological Sciences* 271:2605–2611.
- Mezzetti, B., L. Landi, L. Scortichini, A. Rebori, A. Spena, and T. Pandolfini. 2002a. Genetic engineering of parthenocarpic fruit development in strawberry. *Acta Horticulturae* 567(1):101–104.
- Mezzetti, B., L. Landi, A. Spena, R.M. Brennan, S.L. Gordon, and B. Williamson. 2002b. Biotechnology for improving *Rubus* production and quality. *Acta Horticulturae* (585):73–78.
- Mezzetti, B., L. Landi, T. Pandolfini, and A. Spena. 2004. The *defH9-iaaM* auxin-synthesizing gene increases plant fecundity and fruit production in strawberry and raspberry. *BMC Biotechnology* 4(March 15):4.
- Michener, C.D. 1969. Comparative social behavior of bees. *Annual Review of Entomology* 14:299–342.
- Michener, C.D. 1974. *The Social Behavior of the Bees: A Comparative Study*. Cambridge, Mass.: Belknap Press.
- Michener, C.D. 2000. *Bees of the World*. Baltimore and London: The Johns Hopkins University Press. 913 pp.
- Michez, D., M. Terzo, and P. Rasmont, 2004a. Révision des espèces ouest-paléarctiques du genre *Dasygaster* Latreille 1802 (Hymenoptera, Apoidea, Melittidae). *Linzer Biologische Beiträge* 36(2):847–900.
- Michez, D., P. Patiny, and S. Iserbyt. 2004b. Apoidea remarquables observés dans les Pyrénées-Orientales, France (Hymenoptera, Andrenidae et Melittidae). *Bulletin de la Société entomologique de France* 109(4):379–382.
- Mickleburgh, S.P., A.M. Hutson, and P.A. Racey. 2002. A review of the global conservation status of bats. *Oryx* 36:18–34.
- Milani, N., and G. Della Vedova. 1996. Determination of the LC50 in the mite *Varroa jacobsoni* of the active substances in Perizin® and Cekafix®. *Apidologie* 27:175–184.
- Millennium Ecosystem Assessment. 2005. *Ecosystems and Human Well-Being: Biodiversity Synthesis*. Washington: World Resources Institute.
- Miller, S.E., V.O. Becker, and R. Velez-Angel. 1995. *Podalia bolivari* (Lepidoptera: Megalopygidae): a highly sexually dimorphic neotropical pest. *Proceedings of the Entomological Society of Washington* 97:117–122.
- Minckley, R.L., and S.G. Reyes. 1996. Capture of the orchid bee, *Eulaema polychroma*, (Friese) (Apidae: Euglossini) in Arizona, with notes on northern distributions of other Mesoamerican bees. *Journal of the Kansas Entomological Society* 62(1):102–104.
- Mineau, P., C.M. Downes, D.A. Kirk, E. Bayne, and M. Csizy. 2005. Patterns of bird species abundance in relation to granular insecticide use in the Canadian prairies. *Ecoscience* 12:267–278.
- Minorsky, P.V. 2001. The hot and the classic. *Plant Physiology* 127:709–710.
- Miriti, M.N., S.J. Wright, and H.F. Howe. 2001. The effects of neighbors on a dominant desert shrub (*Ambrosia dumosa*). *Ecological Monographs* 71(4):491–509.
- Mississippi State University Extension Service. 2006. 2002 Annual Report of Mississippi State University Extension Service. Available at: <http://msucares.com/pubs/misc/m1281.html>. Accessed January 2006.
- Mitchell, T.B. 1962. *Bees of the eastern United States, Volume 2*. North Carolina Agricultural Experiment Station Technical Bulletin 152.
- Moeller, D.A. 2004. Facilitative interactions among plants via shared pollinators. *Ecology* 85:3289–3301.
- Molnar, S. 2004. *Plant Reproductive Systems*. Available at: http://www.geocities.com/we_evolve/Plants/breeding_sys.html. Accessed March 10, 2006.

- Mora, J.M., V.V. Mendez, and L.D. Gomez. 1999. White-nosed coati *Nasua narica* (Carnivora: Procyonidae) as a potential pollinator of *Ochroma pyramidale* (Bombacaceae). *Revista de Biología Tropical* 47:719–721.
- Morandin, L.A., and M.L. Winston. 2003. Effects of novel pesticides on bumble bee (Hymenoptera: Apidae) colony health and foraging ability. *Environmental Entomology* 32(3):555–563.
- Morandin, L.A., and M.L. Winston. 2005. Wild bee abundance and seed production in conventional, organic, and genetically modified canola. *Ecological Applications* 15:871–881.
- Morandin, L.A., and M.L. Winston. 2006. Pollinators provide economic incentive to preserve natural land in agroecosystems. *Agriculture Ecosystems and Environment* 116:289–292.
- Morandin, L.A., T.M. Laverty, P.G. Kevan, S. Khosla, and L. Shipp. 2001. Bumble bee (Hymenoptera: Apidae) activity and loss in commercial greenhouses. *Canadian Entomologist* 133:883–893.
- Morandin, L.A., M.L. Winston, M.T. Franklin, and V.A. Abbott. 2005. Lethal and sub-lethal effects of spinosad on bumble bees (*Bombus impatiens* Cresson). *Pest Management Science* 61(7):619–628.
- Moreno, A. 1997. Murciélagos de Nuevo Leon. Grupo IMSA, Monterrey, Mexico.
- Moreno-Valdez, A., R.L. Honeycutt, and W.E. Grant. 2004. Colony dynamics of *Leptonycteris nivalis* (Mexican long-nosed bat) related to flowering agave in Northern Mexico. *Journal of Mammalogy* 85:453–459.
- Moritz, R.F.A. 1985. Heritability of the postcapping stage in *Apis mellifera* and its relation to Varroa resistance. *Journal of Heredity* 76:267–270.
- Moritz, R.F.A., and H. Hanel. 1984. Restricted development of the parasitic mite *Varroa jacobsoni* Oud. in the cape honeybee *Apis mellifera capensis* Esch. *Zeitschrift für Angewandte Entomologie*. 97:91–95.
- Morris, W.F. 2003. Which mutualists are most essential? Buffering of plant reproduction against the extinction of pollinators. P. 427 in *The Importance of Species: Perspectives on Extinction and Triage*, P. Kareiva and S.A. Levin, eds. Princeton: Princeton University Press.
- Morrison, L.W. 2002. Island biogeography and metapopulation dynamics of Bahamian ants. *Journal of Biogeography* 29:387–394.
- Morse, R.A., and N.W. Calderone. 2000. The value of honey bees as pollinators of U.S. crops in 2000. *Bee Culture* 128(3):1–15.
- Morse, R.A., and K. Flottum. 1997. *Honey Bee Pests, Predators, and Diseases*. 3rd edition. Medina, Ohio: The A. I. Root Company. 718 pp.
- Morse, R.A., and L.S. Gonçalves. 1979. Varroa disease, a threat to world beekeeping. *Gleanings in Bee Culture* 107:179–181.
- Morse, R.A. 1994. *The New Complete Guide to Beekeeping*. Woodstock, Vt.: The Countryman Press.
- Mound, L.A. 1997. Biological diversity. Pp. 197–215 (Chapter 6) in *Thrips as Crop Pests*, T. Lewis, ed. Wallingford: CAB International.
- Müller, H. 1869. DeCandolle, *Prodromus systematis naturalis regni vegetabilis* 16:16.
- Müller, H., and F. Delpino. 1869. Application of the Darwinian theory to flowers and the insects which visit them. Translated by R.L. Packard, 1871. *American Naturalist* 5:271–297.
- Muth, M.K., R.R. Rucker, W.N. Thurman, and C-T. Chuang. 2002. The fable of the bees revisited: causes and consequences of the U.S. honey program. *The Journal of Law and Economics* 46:479–516.
- NAPPC (North American Pollinator Protection Campaign). 2006. Reducing Risks to Pollinators from Pesticides. Available at: <http://www.napcc.org/PesticidesMain.html>.
- Nabhan, G.P., and S.L. Buchmann. 1996. Pollination services: biodiversity's direct link to world food stability. In G. Daly, ed. Washington: Ecosystem Services, Island Press.

- Nabhan, G.P., R.C. Brusca, and L. Holter, ed. 2004. Conserving migratory pollinators and nectar corridors in western North America. Tucson: University of Arizona Press.
- Nadel, H., J.H. Frank, and R.J. Knight. 1992. Escapees and accomplices: the naturalization of exotic *Ficus* and their associated faunas in Florida. *Florida Entomologist* 75:29–38.
- Nason, J.D., and J.L. Hamrick. 1997. Reproductive and genetic consequences of forest fragmentation: two case studies of neotropical canopy trees. *Journal of Heredity* 88:264–276.
- Nasr, M.E., G.W. Otis, and C.D. Scott-Dupree. 2001. Resistance to *Acarapis woodi* by honey bees (Hymenoptera: Apidae): divergent selection and evaluation of selection progress. *Journal of Economic Entomology* 94(2):332–338.
- National Plant Board. 2005. Annual Meeting, Biloxi, Mississippi, Resolution No. 7; Florida Department of Agriculture and Consumer Services—Division of Plant Industry. Available at: <http://www.doacs.state.fl.us/pi/plantinsp/apiary/africanbees.html>; Florida Public Advisory, July 11, 2005.
- Neumann, P., and P.J. Elzen. 2004. The biology of the small hive beetle (*Aethina tumida*, Coleoptera: Nitidulidae): gaps in our knowledge of an invasive species. *Apidologie* 35(3):229–247.
- Neuweiler, G. 2000. Biology of Bats. Oxford: Oxford University Press.
- Nilsson, L.A. 1978. Pollination ecology of *Epipactis palustris* (Orchidaceae). *Botaniska Notiser* 131:355–368.
- Niwa, S., H. Iwano, S. Asada, M. Matsuura, and K. Goka. 2004. A microsporidian pathogen isolated from a colony of the European bumblebee, *Bombus terrestris*, and infectivity on Japanese bumblebee. *Japanese Journal of Applied Entomology and Zoology* 48:60–64.
- Norman, E.M., and D. Clayton. 1986. Reproductive biology of two Florida pawpaws; *Asimina ovata* and *A. pygmaea*. *Bulletin of the Torrey Botanical Club* 113:16–22.
- Norton, C. 2005. The price of California's almond pollination—part II of two parts. *American Bee Journal* 145(5):387–389.
- Noss, R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4:355–364.
- Noyes, J.S. 1998. Catalogue of Chalcidoidea of the World. CD-ROM series World Biodiversity Database. Amsterdam, Netherlands: ETI Biodiversity Centre.
- NRC (National Research Council). 1995. Science and the Endangered Species Act. Washington: National Academy Press.
- NRC. 1996. National Science Education Standards. Washington: National Academy Press.
- NRC. 2000. The Future Role of Pesticides in U.S. Agriculture. Washington: National Academy Press.
- NRC. 2005. Valuing Ecosystem Services: Toward Better Environmental Decision-Making. Washington: The National Academies Press.
- NRCC (Natural Resource Council Canada). 1981. Pesticide-Pollinator Interactions. NRCC Report No. 18471. Associate Committee on Scientific Criteria for Environmental Quality. Ottawa: National Research Council of Canada. 190 pp.
- NRCS (Natural Resources Conservation Service). North Dakota. 2005. 2005 Conservation Security Program. Natural Resources Conservation Service—North Dakota, U.S. Department of Agriculture. Available at: http://www.nd.nrcs.usda.gov/programs/CSP/csp_2005.asp. Accessed December 30, 2005.
- NRCS. 2006a. Wildlife Habitat Incentives Program. U.S. Department of Agriculture. Available at: <http://www.nrcs.usda.gov/programs/whip/>. Accessed March 10, 2006.
- NRCS. 2006b. Environmental Quality Incentives Program. U.S. Department of Agriculture. Available at: <http://www.nrcs.usda.gov/programs/eqip/>. Accessed March 10, 2006.
- NRCS. 2006c. Conservation Security Program. U.S. Department of Agriculture. Available at: <http://www.nrcs.usda.gov/programs/csp/>. Accessed March 10, 2006.

- Oberhauser, K., M.D. Prysby, H.R. Mattila, D.E. Stanley-Horn, M.K. Sears, G. Dively, E. Olson, J.M. Pleasants, W.-K.F. Lam, and R.L. Hellmich. 2001. Temporal and spatial overlap between monarch larvae and corn pollen. *Proceedings of the National Academy of Sciences USA* 98:11913–11918.
- O'Brien, J.M., M.L. Rosenzweig, J.H. Thorne, and A.M. Shapiro. Forthcoming (in revision). A cryptic decline of butterfly species diversity near Davis, California. *Diversity and Distributions*.
- O'Brien, T.G., and M.F. Kinnaird. 2003. Caffeine and conservation. *Science* 300:587.
- O'Callaghan, M., T.R. Glare, E.P.J. Burgess, and L.A. Malone. 2005. Effects on plants genetically modified for insect resistance on nontarget organisms. *Annual Review of Entomology* 50:271–292.
- Oldroyd, B.P., and S. Wongsiri. 2006. *Asian Honey Bees: Biology, Conservation, and Human Interactions*. Cambridge, Mass.: Harvard University Press.
- Olesen, J.M., and S.K. Jain. 1994. Fragmented plant populations and their lost interactions. Pp. 417–426 in *Conservation Genetics*, V. Loeschcke, J. Tomiuk, and S.K. Jain, eds. Basel, Switzerland: Birkhauser Verlag.
- O'Neill, K.M., H.E. Evans, and L.B. Bjostad. 1991. Territorial behaviour in males of three North American species of bumble bees (Hymenoptera: Apidae, *Bombus*). *Canadian Journal of Zoology* 69:604–613.
- Ornelas, J.F. 2000. Apodiformes: Trochilidae. Pp. 252–262 in *Las Aves de México en Peligro de Extinción*, G. Ceballos y L. Márquez Valdelamar, eds. UNAM, CONABIO, Fondo de Cultura Económica, México, D.F.
- Ornelas, J.F., M. Ordano, A. Hernandez, J.C. Lopez, L. Mendoza, and Y. Perroni. 2002. Nectar oasis produced by *Agave marmorata* Roehl. (Agavaceae) lead to spatial and temporal segregation among nectarivores in the Tehuacan Valley, Mexico. *Journal of Arid Environments* 52:37–51.
- Ortega-Rivas, C., and R. Ochoa-Bautista. 2004. La producción de miel en México: Modernidad y Tradición. *Claridades Agropecuarias* 128:3–13. Available at: <http://www.infoasercar.gob.mx/claridades/revistas/128/ca128.pdf>. Accessed March 6, 2006.
- Otis, G.W. 1990. Results of a survey on the economic impact of tracheal mites. *American Bee Journal* 130:28–31.
- O'Toole, C. 1993. Diversity of native bees and agroecosystems. Pp. 69–106 in *Hymenoptera and Biodiversity*, J. LaSalle and I. Gauld, eds. Wallingford: CAB International.
- O'Toole, C. 1994. Who cares for solitary bees? Pp. 47–56 in *Forage for Bees in an Agricultural Landscape*, A. Matheson, ed. Cardiff: International Bee Research Association.
- O'Toole, C., ed. 2002. *The New Encyclopedia of Insects and their Allies*. Oxford: Oxford University Press. 240 pp.
- O'Toole, C., and A. Raw. 1991. *Bees of the World*. London: Blandford Publishing, 191 pp.
- Otterstatter, M.C., R.J. Gegeer, S.R. Colla, and J.D. Thomson. 2005. Effects of parasitic mites and protozoa on the flower constancy and foraging rate of bumble bees. *Behavioral Ecology and Sociobiology* 58:383–389.
- Oudemans, A.C. 1904. Acarological notes xiii. *Entomologische berichten uitgegeven door de Nederlandsche Entomologische Vereeniging* 1:169–174.
- Page, R.E., Jr., and N.E. Gary. 1990. Genotypic variation in susceptibility of honey bees (*Apis mellifera*) to infestation by tracheal mites (*Acarapis woodi*). *Experimental and Applied Acarology* 8:275–283.
- Page, R.E., Jr., and H.H. Laidlaw, Jr. 1982a. Closed population honeybee breeding. I. Population genetics of sex determination. *Journal of Apicultural Research* 21:30–37.
- Page, R.E., Jr., and H.H. Laidlaw, Jr. 1982b. Closed population honeybee breeding. II. Comparative methods of stock maintenance and selective breeding. *Journal of Apicultural Research* 21:38–44.

- Page, R.E., Jr., and H.H. Laidlaw, Jr. 1992. Honey bee genetics and breeding. Pp. 235–267 in *The Hive and the Honey Bee*. Hamilton, Ill.: Dadant and Sons.
- Page, R.E., Jr., H.H. Laidlaw, Jr., and E.H. Erickson, Jr. 1983. Closed population honeybee breeding 3. The distribution of sex alleles with gyne supersedure. *Journal of Apicultural Research* 22:184–190.
- Page, R.E., Jr., H.H. Laidlaw, Jr., and E.H. Erickson, Jr. 1985. Closed population honeybee breeding 4. The distribution of sex alleles with top crossing. *Journal of Apicultural Research* 24:38–42.
- Pagnotta, M.A. 1999. Genetic engineering of parthenocarpic vegetable crops. Pp. 301–306 in *Genetics and Breeding for Crop Quality and Resistance*, Proceedings of the XV EU-CARPIA Congress, Viterbo, Italy, September 20–25, 1998. Dordrecht, Germany: Kluwer Academic Publishers.
- Pankiw, T. 2004. Brood pheromone regulates foraging activity of honey bees (Hymenoptera: Apidae). *Journal of Economic Entomology* 97(3):748–751.
- Park, O.W. 1936. Disease resistance and American foulbrood. *American Bee Journal* 76:12–15.
- Park, O.W., F.C. Pellett, and F.B. Paddock. 1937. Disease resistance and American foulbrood. Results of 2nd season of cooperative experiment. *American Bee Journal* 77(34):20–25.
- Park, O.W., F.C. Pellett, and F.B. Paddock. 1939. Results of Iowa's 1937–1938 honeybee disease resistance program. *American Bee Journal* 79:577–582.
- Parker, F.D. 1981. How efficient are bees in pollinating sunflowers? *Journal of the Kansas Entomological Society* 54(1):61–67.
- Parmesan, C., N. Ryrholm, C. Stefanescu, J.K. Hill, C.D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W.J. Tennent, J.A. Thomas, and M. Warren. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399:579–583.
- Patiny, S. 1998. Contribution à la connaissance de la régression des populations du sous-genre *Taeniandrena* Hedicke 1933 (Hym., Andrenidae, *Andrena*) et leurs habitudes pollinisatrices. *Notes fauniques de Gembloux* 35:20–33.
- Patiny, S., and C. Gaspar. 2000. Biogéographie des *Melitturga* Latreille 1809, *Melitturga* Friese, 1903 et des genres proches (Hymenoptera: Andrenidae, Panurginae). *Notes fauniques de Gembloux* 39:3–44.
- Paton, D.C. 1990. Budgets for the use of floral resources in mallee heath. Pp. 189–193 in *The Mallee Lands: A Conservation Perspective*, J.C. Noble, P.J. Joss and G.K. Jones, eds. Melbourne: CSIRO.
- Paton, D.C. 1993. Honeybees *Apis mellifera* in the Australian environment. Does *Apis mellifera* disrupt or benefit native biota? *Bioscience* 43:95–103.
- Paton, D.C. 1996. Overview of Feral and Managed Honeybees in Australia: Distribution, Abundance, Extent of Interactions with Native Biota, Evidence of Impacts and Future Research. Canberra: Australian Nature Conservation Agency. Available at: <http://www.deh.gov.au/biodiversity/invasive/publications/bees/introduction.html>. Accessed May 22, 2006.
- Paton, D.C., L. Jansen, and D. Oliver. 1992. Interactions between honeybees and Australian biota on Kangaroo Island.
- Pauly, A. 1999. Catalogue des Hyménoptères Aculéates de Belgique. *Bulletin de la Société royale belge d'Entomologie* 135:98–125.
- Pauly, A., R.W. Brooks, L.A. Nilsson, Y.A. Pesenko, C.D. Eardley, M. Terzo, T. Griswold, M. Schwarz, S. Patiny, J. Munzinger, and Y. Barbier. 2001. Hymenoptera Apoidea de Madagascar et des îles voisines. *Annales du Musée royal de l'Afrique centrale (Sciences Zoologiques)*, Tervuren (Belgique) 286:1–406.

- Peakall, R., S.N. Handel, and A.J. Beattie. 1991. The evidence for, and importance of, ant pollination. Pp. 421–429 in *Ant-Plant Interactions*, C.R. Huxley and D.F. Cutler, eds. Oxford: Oxford University Press.
- Pearson, D.L., and R.L. Dressler. 1985. Two-year study of male orchid bee (Hymenoptera: Apidae: Euglossini) attraction to chemical baits in lowland south-eastern Peru. *Journal of Tropical Ecology* 1:37–54.
- Pellmyr, O. 2003. Yuccas, yucca moths, and coevolution: a review. *Annals of the Missouri Botanical Garden* 90:35–55.
- Pellmyr, O., J.N. Thompson, J.M. Brown, and R.G. Harrison. 1996. Evolution of pollination and mutualism in the yucca moth lineage. *American Naturalist* 148:827–847.
- Peñuelas, J., I. Filella, and P. Comas. 2002. Changed plant and animal life cycles from 1952–2000 in the Mediterranean region. *Global Change Biology* 8:531–544.
- Peterson, S.S., C.R. Baird, and R.M. Bitner. 1992. Current status of the alfalfa leafcutting bee, *Megachile rotundata*, as a pollinator of alfalfa seed. *Bee Science* 3:135–142.
- Pettis, J.S., and H. Shimanuki. 1999. A hive modification to reduce varroa populations. *American Bee Journal* 139:471–473.
- Pettis, J.S., W.T. Wilson, F.A. Eischen, and A. Suarez. 1987. Distribution of *Acarapis woodi* among rustic and modern honey bee hives in northeast Mexico. *American Bee Journal* 127(12):849.
- Pettis, J.S., A.M. Collins, R. Wilbanks, and M.F. Feldlaufer. 2004. Effects of coumaphos on queen rearing in the honey bee, *Apis mellifera*. *Apidologie* 35:605–610.
- Pham-Delègue, M.-H, A. Decourtye, L. Kaiser, and J. Devillers. 2002. Behavioural methods to assess the effects of pesticides on honey bees. *Apidologie* 33:425–432.
- Phillips, J.R., J.B. Graves, and R.G. Luttrell. 1989. Insecticide resistance management: relationship to integrated pest management. *Pesticide Science* 27(4):459–464.
- Pickett, C.H., and R.L. Bugg. 1998. Introduction: enhancing biological control-habitat management to promote natural enemies of agricultural pests. Pp. 1–24 in *Enhancing Biological Control*, C.H. Pickett and R.L. Bugg, eds. Berkeley: University of California Press.
- Pickett, S.T.A., and P.S. White. 1985. Natural disturbance and patch dynamics: an introduction. Pp. 3–13 in *The Ecology of Natural Disturbance and Patch Dynamics*, S.T.A. Pickett and P.S. White, eds. Orlando: Academic Press.
- Pierson, E.D. 1998. Tall trees, deep holes, and scarred landscapes: conservation biology of North American bats. Pp. 309–325 in *Bats: Phylogeny, Morphology, Echolocation, and Conservation Biology*, T.H. Kunz and P.A. Racey, eds. Washington: Smithsonian Institution Press.
- Pimm, S.L., M.P. Moulton, and L.J. Justice. 1994. Bird extinctions in the central Pacific. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences* 344:27–33.
- Pleasants, J.M., R.L. Hellmich, G. Dively, M.K. Sears, D.E. Stanley-Horn, H.R. Mattila, J.E. Foster, P.L. Clark, and G.D. Jones. 2001. Corn pollen deposition on milkweeds in and near cornfields. *Proceedings of National Academy of Sciences USA* 98(21):11919–11924.
- Plowright, C. 1996. Bumble bee rearing. *Melissa* 9:10–12.
- Plowright, R.C., B.A. Pendrel, and I.A. McLaren, 1978. The impact of aerial fenitrothion spraying upon the population biology of bumble bees (*Bombus* Latr.: Hym.) in south western New Brunswick. *Canadian Entomologist* 110(11):1145–1156.
- Pollack, S., and A. Perez. 2005. Fruit and Tree Nuts Situation and Outlook Yearbook. FTS–2005. Washington: U.S. Department of Agriculture, Economic Research Service. Available at: <http://www.ers.usda.gov/publications/so/view.asp?f=/specialty/fts-bb/>.
- Potts, S.G., P. Willmer, A. Dafni, and G. Ne’eman. 2001. The utility of fundamental ecological research of plant-pollinator interactions as the basis for landscape management practices. VIII International Symposium on Pollination—Pollination: Integrator of Crops and Native Plant Systems. *ISHS Acta Horticulturae* 561:141–144.

- Potts, S.G., B. Vulliamy, A. Dafni, G. Ne'eman, C. O'Toole, S. Roberts, and P.G. Willmer. 2003. Response of plant-pollinator communities following fire: changes in diversity, abundance and reward structure. *Oikos* 101:103–112.
- Potts, S.G., P.G. Kevan, and J.W. Boone. 2005. Conservation in pollination: collecting, surveying and monitoring. Pp. 401–434 in *Pollination Ecology: A Practical Approach*, A. Dafni and P. Kevan, eds. Cambridge, Canada: Enviroquest.
- Potts, S.G., R.B. Bradbury, S.R. Mortimer, and B.A. Woodcock. 2006. Commentary on Kleijn et al., 2006, *Ecology Letters* 9(3):254–256.
- Powell, J.A. 1992. Interrelationships of yuccas and yucca moths. *Trends in Ecology and Evolution* 7:10–15.
- Powell, J.A., C. Mitter, and B.D. Farrell. 1998. Evolution of larval food preferences in Lepidoptera. Pp. 403–422 in *Handbook of Zoology, Part 35, Vol. 1. Evolution, Systematics and Biogeography*, N. Kristensen, ed. New York: de Gruyter.
- Power, A.G., and C.E. Mitchell. 2004. Pathogen spillover in disease epidemics. *American Naturalist* 164:179–189.
- Prescott-Allen, C., and R. Prescott-Allen. 1986. *The First Resource: Wild Species in the North American Economy*. New Haven: Yale University Press.
- Prescott-Allen, R., and C. Prescott-Allen. 1990. How many plants feed the world? *Conservation Biology* 4:365–374.
- Price, M.V., N.M. Waser, R.E. Irwin, D.R. Campbell, and A.K. Brody. 2005. Temporal and spatial variation in pollination of a montane herb: a seven-year study. *Ecology* 86:2106–2116 (B-56).
- Primack, D., C. Imbres, R.B. Primack, A.J. Miller-Rushing, and P. Del Tredici. 2004. Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany* 91:1260–1264.
- Procter, W. 1946. *Biological Survey of the Mount Desert Region, Part VII. The Insect Fauna with Reference to Methods of Capture, Food Plants, the Flora and Other Biological Factors*. Philadelphia: Wistar Institute, 566 pp.
- Proctor, M., P. Yeo, and A. Lack. 1996. *The Natural History of Pollination*. Portland: Timber Press.
- Prys-Jones, O.E., and S.A. Corbet. 1987. *Bumblebees*. Cambridge: Cambridge University Press.
- Puterbaugh, M.N. 1998. The roles of ants as flower visitors: experimental analysis in three alpine species. *Oikos* 83:36–46.
- Pyke, G.H., and N.M. Waser. 1981. The production of dilute nectars by hummingbird and honeyeater flowers. *Biotropica* 13:260–270.
- Pywell, R.F., E.A. Warman, T.H. Sparks, J.N. Greatorex-Davis, K.J. Walker, W.R. Meek, C. Carvell, S. Petit, and L.G. Firbank. 2004. Assessing habitat quality for butterflies on intensively managed farmland. *Biological Conservation* 118:313–325.
- Pywell, R.F., E.A. Warman, C. Carvell, T.H. Sparks, L.V. Dicks, D. Bennett, A. Wright, C.N.R. Critchley, and A. Sherwood. 2005. Providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation* 121:479–494.
- Pywell, R.F., E.A. Warman, L. Hulmes, S. Hulmes, P. Nuttall, T.H. Sparks, C.N.R. Critchley, and A. Sherwood. 2006. Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation* 129(2):192–206.
- Quesada, M., K.E. Stoner, V. Rosas-Guerrero, C. Palacios-Guevara, and J.A. Lobo. 2003. Effects of habitat disruption on the activity of nectarivorous bats (Chiroptera: Phyllostomidae) in a dry tropical forest: implications for the reproductive success of the neotropical tree *Ceiba grandiflora*. *Oecologia* 135:400–406.

- Raguso, R.A., C. Henzel, S.L. Buchmann, and G.P. Nabhan. 2003. Trumpet flowers of the Sonoran Desert: floral biology of *Peniocereus* cacti and Sacred Datura. *International Journal of Plant Sciences* 164:877–892.
- Ramírez, V. 1998. Inventario revela existencia de 203 millones de plantas. Pp. 163–164 in *Foro de Análisis de la problemática de la cadena productiva agave tequila*. Guadalajara, México: Consejo Regulador del Tequila.
- Rappole, J.H., and M.V. McDonald. 1994. Cause and effect in migratory bird population changes. *Auk* 111:652–660.
- Rasmont, P., and A. Adamski. 1995. Bumblebees of Corsica (Hymenoptera, Apoidea, Bombinae). *Faunal Notes of Gembloux* 31:3–87.
- Rasmont, P., and Y. Barbier. 2003. Biodiversité du Maroc. Available at: <http://zoologie.umh.ac.be/marocbiotax/div/taxon.asp?parentID=2094&fiche=false>.
- Rasmont, P., and D. Flagothier, 1996. Biogéographie et choix floraux des bourdons (Hymenoptera, Apidae) de la Turquie. Rapport préliminaire O.T.A.N.-N.A.T.O. 1995–1996. Université de Mons-Hainaut, Mons, Belgique, 69 + III pp.
- Rasmont, P., and C. Gaspar, eds. 2002. *Atlas Hymenoptera*. Available at: <http://zoologie.umh.ac.be/hymenoptera/>.
- Rasmont, P., and P. Mersch. 1988. Première estimation de la dérive faunique chez les bourdons de la Belgique (Hymenoptera: Apidae). *Annales de la Société royale zoologique de Belgique* 118:141–147.
- Rasmont, P., J. Leclercq, A. Jacob-Remacle, A. Pauly, and C. Gaspar. 1993. The faunistic drift of Apoidea in Belgium. Pp. 65–87 in *Bees for Pollination*, E. Bruneau, ed. Brussels: Commission of the European Communities. 237 pp.
- Rasmont, P., P.A. Ebmer, J. Banaszak, and G. van der Zanden. 1995. Hymenoptera Apoidea Gallica. Taxonomic list of the bees of France, of Belgium, of Switzerland and the Grand Duchy of Luxembourg. *Bulletin of the Entomological Company of France*, 100(excerpt series):1–98.
- Rasmont, P., A. Pauly, M. Terzo, S. Patiny, D. Michez, S. Iserbyt, Y. Barbier, and E. Haubruge. 2006. The survey of wild bees (Hymenoptera, Apoidea) in Belgium and France. In *Status of the World's Pollinators*. Rome: Food and Agriculture Organisation of the United Nations. 18 pp.
- Rasmussen, K.K., and J. Kollmann. 2004. Pollen limitation and inbreeding depression in the rare tree *Sorbus torminalis*. *Acta Oecologica* 25:211–218.
- Rasplus, J.Y., C. Kerdelhué, I. Le Clainche, and G. Mondor. 1998. Molecular phylogeny of fig waps (Hymenoptera). Agaonidae are not monophyletic. *Compte Rendu de l'Académie des Sciences de Paris* 321:517–527.
- Rath, W. 1999. Co-adaptation of *Apis cerana* Fabr. and *Varroa jacobsoni* Oud. *Apidologie* 30:97–110.
- Rathcke, B.J., and E.S. Jules. 1993. Habitat fragmentation and plant-pollinator interactions. *Current Science* 65:273–277.
- Ratnieks, F.L.W. 1992. American foulbrood: the spread and control of an important disease of the honey bee. *Bee World* 73:177–191.
- Rausser, G., and A. Small. 2000. Valuing research leads: bioprospecting and the conservation of genetic resources. *Journal of Political Economy* 108(1):173–206.
- Raven, P.H., R.F. Evert, and S.E. Eichhorn. 2005. *Biology of Plants*. New York: W.H. Freeman and Company.
- Reid, F.A. 1997. *A field guide to the mammals of Central America and southeast Mexico*. New York: Oxford University Press. 334 pp.
- Renner, S.S., and K.A. Johanson. 1995. Breeding system and pollination of *Nuphar luteum* (L.) Smith (Nymphaeaceae) in Norway. *Flora* 190:109–113.
- Rennie, J. 1921. Notes on Acarine disease. *Bee World* 2:144–145.

- Riba-Hernandez, P., and K.E. Stoner. 2005. Massive destruction of *Symphonia globulifera* (Clusiaceae) flowers by Central American spider monkeys (*Ateles geoffroyi*). *Biotropica* 37:274–278.
- Richards, A.J. 1997. *Plant Breeding Systems*. 2nd edition. London: Garland Science.
- Richards, C.S., M.P. Hill, and J.F. Dames. 2005. The susceptibility of small hive beetle (*Aethina tumida* Murray) pupae to *Aspergillus niger* (van Tieghem) and *A. flavus* (Link:Grey). *American Bee Journal* 145(9):748–751.
- Richards, K.W. 2003. Potential use of the alfalfa leafcutter bee *Megachile rotundata* to pollinate sweet clover. *Journal of Apicultural Research* 42(1/2):21–24.
- Richards, O.W. 1963. *The Species of Pseudomasaris Ashmead*. Berkeley: University of California Press. 28 pp.
- Richards, O.W. 1966. New Records of *Pseudomasaris Ashmead* (Hymenoptera: Vespoidea, Masaridae), with notes on *P. phaceliae* Rohwer and *P. cazieri* R.M. Bohart. *Proceedings of the Royal Society of London Series B—Biological Sciences* 35:47–55.
- Richardson, D.M., R.M. Cowling, and B.B. Lamont. 1996. Non-linearities, synergisms and plant extinctions in South African fynbos and Australian kwongan. *Biodiversity Conservation* 5(9):1035–1046.
- Ricketts, T.H. 2001. The matrix matters: effective isolation in fragmented landscapes. *American Naturalist* 158:87–99.
- Ricketts, T.H. 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conservation Biology* 18:1262–1271.
- Ricketts, T.H., E. Dinerstein, D.M. Olson, C.J. Loucks, W. Eichbaum, D. DellaSala, K. Kavanagh, P. Hedao, P.T. Hurley, K.M. Carney, R. Abell, and S. Walters. 1999. *Terrestrial Ecoregions of North America: A Conservation Assessment*. Washington: Island Press.
- Ricketts, T.H., G.C. Daily, P.R. Ehrlich, and C.D. Michener. 2004. Economic value of tropical forest to coffee production. *Proceedings of the National Academy of Sciences USA* 101:12579–12582.
- Rico-Gray, V., and P.S. Oliveira. 2006. *Ecology of Ant-Plant Interactions*. Chicago: University of Chicago Press.
- Rinderer, T.E. 1986. Africanized bees: the Africanization process and potential range in the United States. *Bulletin of the Entomological Society of America* Winter:222–227.
- Rinderer, T.E., L.I. de Guzman, V.A. Lancaster, G.T. Delatte, and A. Stelzer. 1999. *Varroa* in the mating yard: I. The effects of *Varroa jacobsoni* and Apistan on drone honey bees. *American Bee Journal* 28:134–139.
- Rinderer, T.E., L.I. de Guzman, G.T. Delatte, J.A. Stelzer, V.A. Lancaster, V. Kuznetsov, L. Beaman, R. Watts, and J.W. Harris. 2001. Resistance to the parasitic mite *Varroa destructor* in honey bees from far-eastern Russia. *Apidologie* 32:381–394.
- Rinderer, T.E., L.I. de Guzman, G.T. Delatte, and C. Harper. 2003. An evaluation of ARS Russian honey bees in combination with other methods for the control of varroa mites. *American Bee Journal* 143:410–413.
- Rinderer, T.E., L.I. de Guzman, and R. Danka. 2005. A new phase begins for the USDA-ARS Russian Honey Bee Breeding Program. *American Bee Journal* 145:579–582.
- Robbins, C.S., J.R. Sauer, R.S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the neotropics. *Proceedings of the National Academy of Sciences USA* 86(19):7658–7662.
- Roberts, D.L., R.J. Cooper, and L.J. Petit. 2000. Use of premontane moist forest and shade coffee agroecosystems by army ants in western Panama. *Conservation Biology* 14:192–199.
- Roberts, R.B. 1978. The nesting biology, behavior and immature stages of *Lithurge chrysurus*, an adventitious wood-boring bee in New Jersey (Hymenoptera: Megachilidae). *Journal of Kansas Entomological Society* 51:735–745.
- Robertson, A.W., D. Kelly, J.J. Ladley, and A.D. Sparrow. 1999. Effects of pollinator loss on endemic New Zealand mistletoes (Loranthaceae). *Conservation Biology* 13:499–508.

- Robertson, C. 1929. Flowers and Insects. Lists of Visitors to Four Hundred and Fifty-Three Flowers. Lancaster, Pa.: Science Press Printing Company.
- Robinson, G.E. 1992. The regulation of division of labor in insect societies. *Annual Review of Entomology* 37:637–665.
- Robinson, G.E., and F.L.W. Ratnieks. 1987. Induction of premature honey bee (Hymenoptera: Apidae) flight by juvenile hormone analogs administered orally or topically. *Journal of Economic Entomology*. 80:784–787.
- Robinson, G.E., C.M. Grozinger, and C.W. Whitfield. 2005. Sociogenomics: social life in molecular terms. *Nature Reviews Genetics* 6:257–270.
- Robinson, W.S., R. Nowogrodzki, and R.A. Morse. 1989a. The value of honey bees as pollinators of U.S. crops. Part I of a two-part series. *American Bee Journal* 129:411–423.
- Robinson, W.S., R. Nowogrodzki, and R.A. Morse. 1989b. The value of honey bees as pollinators of U.S. crops. Part II of a two-part series. *American Bee Journal* 129:477–487.
- Rocha, M., A. Valera, and L.E. Eguiarte. 2005. Reproductive ecology of five sympatric *Agave littaea* (Agavaceae) species in Central Mexico. *American Journal of Botany* 92:330–341.
- Rodman, J.E., and J.H. Cody. 2003. The taxonomic impediment overcome: NSF's partnerships for enhancing expertise in taxonomy (PEET) as a model. *Systematic Biology* 52:428–435.
- Rogg, K.A., O.R. Taylor, and D.L. Gibo. 1999. Mark and recapture during the monarch migration: a preliminary analysis. Pp. 133–138 in 1997 North American Conference on the Monarch butterfly, J. Hoth, L. Merino, L. Oberhauser, I. Piscanty, S. Price, and T. Wilkinson, eds. Quebec: Commission for Environmental Cooperation.
- Rothenbuhler, W.C. 1964. Behavioral genetics of nest cleaning in the honeybee. I. Response of four inbred lines to disease-killed brood. *Animal Behavior* 4:578–583.
- Rotino, G.L., E. Perri, M. Zottini, H. Sommer, and A. Spena. 1997. Genetic engineering of parthenocarpic plants. *Nature Biotechnology* 15(13):1398–1401.
- Roubik, D.W. 1978. Competitive interactions between neotropical pollinators and Africanized honey bees. *Science* 201:1030–1032.
- Roubik, D.W. 1980. Foraging behavior of competing africanized honeybees and stingless bees. *Ecology* 61(4):836–845.
- Roubik, D.W. 1983. Experimental community studies: Time-series tests of competition between African and Neotropical bees. *Ecology* 64:971–987.
- Roubik, D.W. 1989. *Ecology and Natural History of Tropical Bees*. New York: Cambridge University Press.
- Roubik, D.W., ed. 1995. *Pollination of Cultivated Plants in the Tropics*. Food and Agriculture Organization Agricultural Services Bulletin 118. 196 pp.
- Roubik, D.W. 2001. Ups and downs in pollinator populations: when is there a decline? *Conservation Ecology* 5(1):2.
- Roubik, D.W. 2002. The value of bees to the coffee harvest. *Nature* 417:708.
- Roubik, D.W., and P.E. Hanson. 2004. *Orchid Bees of Tropical America: Biology and Field Guide*. Heredia, Costa Rica: INBIO.
- Roubik, D.W., and H. Wolda. 2001. Do competing honey bees matter? Dynamics and abundance of native bees before and after honey bee invasion. *Population Ecology* 43(1):53–62.
- Roulston, T.H., and J.H. Cane. 2000. Pollen nutritional content and digestibility for animals. *Plant Systematics and Evolution* 222(1–4):187–209.
- Roulston, T.H., J.H. Cane, and S.L. Buchmann. 2000. What governs the protein content of pollen grains: pollinator preferences, pollen-pistil interactions, or phylogeny? *Ecological Monographs* 70:617–643.
- Roy, D.B., and T.H. Sparks. 2000. Phenology of British butterflies and climate change. *Global Change Biology* 6:407–416.

- Roy, D.B., P. Rothery, D. Moss, E. Pollard, and J.A. Thomas. 2001. Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology* 70(2):201–217.
- Roy, D.B., D.A. Bohan, A.J. Houghton, M.O. Hill, J.L. Osborne, S.J. Clark, J.N. Perry, P. Rothery, R.J. Scott, D.R. Brooks, G.T. Champion, C. Hawes, M.S. Heard, and L.G. Firbank. 2003. Invertebrates and vegetation of field margins adjacent to crops subject to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. *Philosophical Transactions of the Royal Society of London B—Biological Sciences* 358:1879–1898.
- Rucker, R.R., W.N. Thurman, and M. Burgett. 2005. Internalizing Reciprocal Benefits: The Economics of Honeybee Pollination Markets. North Carolina State University, Department of Agricultural and Resource Economics, Raleigh, NC, March 6, 2005. Unpublished manuscript. Available at: http://legacy.ncsu.edu:8020/classes/ecg701001/personal/Internalization_of_Reciprocal_Benefits-full_March_2005.pdf.
- Russell, K.N., H. Ikerd, and S. Droege. 2005. The potential conservation value of unmowed powerline strips for native bees. *Biological Conservation* 124:133–148.
- Russell, R.W., F.L. Carpenter, M.A. Hixon, and D.C. Paton. 1994. The impact of variation in stopover habitat quality on migrant Rufous hummingbirds. *Conservation Biology* 8:483–490.
- Rust, R.W. 1974. The systematics and biology of the genus *Osmia*, subgenera *Osmia*, *Chalcosmia*, and *Cephalosmia* (Hymenoptera: Megachilidae). *Wasmann Journal of Biology* 32:1–93.
- Saavedra F., D.W. Inouye, M.V. Price, and J. Harte. 2003. Changes in flowering and abundance of *Delphinium nuttallianum* (Ranunculaceae) in response to a subalpine climate warming experience. *Global Change Biology* 9:885–894.
- SAGARPA. 2005. Estadísticas: Estimación de Consumo Nacional Aparente: Miel de Abeja. Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación. Available at: <http://www.sagarpa.gob.mx/Dgg/CNAmiel.htm> (last updated March 16, 2005). Accessed March 6, 2006.
- Sammataro, D., U. Gerson, and G. Needham. 2000. Parasitic mites of honey bees: life history, implications, and impact. *Annual Review of Entomology* 45:519–548.
- Sampson, B.J., and J.H. Cane. 1999. Impact of enhanced ultraviolet-B radiation on flower, pollen, and nectar production. *American Journal of Botany* 86:108–114.
- Sampson, B.J., and J.H. Cane. 2000. Pollination efficiencies of three bee (Hymenoptera: Apoidea) species visiting rabbiteye blueberry. *Journal of Economic Entomology* 93(6):1726–1731.
- Sampson, B.J., S.J. Stringer, J.H. Cane, and J.M. Spiers. 2004. Screenhouse evaluations of a mason bee *Osmia ribifloris* (Hymenoptera: Megachilidae) as a pollinator for blueberries in the southeastern United States. *Small Fruits Review* 3(3–4):381–392.
- Sárospataki, M., J. Novák, and V. Molnár. 2005. Assessing the threatened status of bumble bee species (Hymenoptera: Apidae) in Hungary, Central Europe. *Biodiversity and Conservation* 14:2437–2446.
- Saskatchewan Agriculture and Food. 2004. A brief history of beekeeping in Saskatchewan. Available at: http://www.agr.gov.sk.ca/docs/crops/apiculture/History_Beekeeping.pdf. Accessed May 16, 2006.
- Sauer, J.R., J.E. Hines, and J. Fallon. 2005. The North American Breeding Bird Survey, Results and Analysis 1966–2005. Version 6.2.2006. Laurel, Md.: USGS Patuxent Wildlife Research Center. Available at: <http://www.mbr-pwrc.usgs.gov/bbs/bbs2005.html>.
- Saville, N.M., W.E. Dramstad, G.L.A. Fry, and S.A. Corbet. 1997. Bumblebee movement in a fragmented agricultural landscape. *Agriculture Ecosystems and Environment* 61:145–154.

- Schaffer, W.M., D.B. Jenson, D.E. Hobbs, J. Gurevitch, J.R. Todd, and M.V. Schaffer. 1979. Competition, foraging energetics and the cost of sociality in three species of bees. *Ecology* 60:976–987.
- Schaffer, W.M., D.W. Zeh, S.L. Buchmann, S. Kleinhaus, M.V. Schaffer, and J. Antrim. 1983. Competition for nectar between introduced honeybees and native North American bees and ants. *Ecology* 64:564–577.
- Schell, R. 2005. A big win for beekeepers. *American Bee Journal* 145:392–394.
- Schery, R.W. 1972. *Plants for Man*. 2nd edition. Englewood Cliffs: Prentice-Hall.
- Schiff, N.M., and W.S. Sheppard. 1995. Genetic analysis of commercial honey bees (Hymenoptera: Apidae) from the southeastern United States. *Journal of Economic Entomology* 88(5):1216–1220.
- Schiff, N.M., and W.S. Sheppard. 1996. Genetic differentiation in the queen breeding population of the western United States. *Apidologie* 27:77–86.
- Schiff, N.M., W.S. Sheppard, G.R. Loper, and H. Shimanuki. 1994. Genetic diversity of feral honey bee (Hymenoptera: Apidae) populations in the southern United States. *Annals of the Entomological Society of America* 87:842–848.
- Schlosser, W., K. Blatner, and R. Chapman. 1991. Economic and marketing implications of special forest products harvest in coastal Pacific Northwest. *Western Journal of Applied Forestry* 6:67–72.
- Schneider, E.L., J. Buchanan, and L.A. Moore. 1977. Morphological studies of the Nymphaeaceae VII. The floral biology of *Nuphar lutea* subsp. *macrophylla*. *Brittonia* 29:88–99.
- Schneider, P. 1986. The influence of *Varroa* infestation during pupal development on the flight activity of the worker honey bees. *Apidologie* 17:366–368.
- Schneider, P., and W. Drescher. 1987. Einfluss der parasitierung durch die Milbe *Varroa jacobsoni* Oud. auf da Schlupfgewicht, die Gewichsentwicklung, die Entwicklung der Hypopharynxdrüsen und die Lebensdauer von *Apis mellifera* L. *Apidologie* 18:101–110.
- Schneider, S.S., G. Degrandi-Hoffman, and D.R. Smith. 2004. The African honey bee: factors contributing to a successful biological invasion. *Annual Review of Entomology* 49:351–376.
- Schondube, J.E., S. Contreras-Martinez, I. Ruan-Tejeda, W.A. Calder, and E. Santana. 2004. Migratory patterns of the rufous hummingbird in western Mexico. Pp. 80–95 in *Conservation of Migratory Pollinators and Their Nectar Corridors in North America*, G. Nabhan, R. C. Brusca, and L. Holter, eds. Arizona–Sonora Desert Museum, Natural History of the Sonoran Desert Region, No. 2. Tucson: University of Arizona Press.
- Schulke, B., and N.M. Waser. 2001. Long-distance pollinator flights and pollen dispersal between populations of *Delphinium nuttallianum*. *Oecologia* 127:239–245.
- Schultz, C.B., and K. Dlugosch. 1999. Nectar and hostplant scarcity limit populations of an endangered Oregon butterfly. *Oecologia* 119:231–238.
- Schurch, S., M. Pfunder, and B.A. Roy. 2000. Effects of ants on the reproductive success of *Euphorbia cyparissias* and associated pathogenic rust fungi. *Oikos* 88:6–12.
- Scott, J.A. 1986. *Butterflies of North America*. Stanford: Stanford University Press. 583 pp.
- Scott-Dupree, C.D., and G.W. Otis. 1992. The efficacy of four miticides for the control of *Acarapis woodi* (Rennie) in a fall treatment program. *Apidologie* 23(2):97–106.
- Scott-Dupree, C.D., and M.L. Winston. 1987. Wild bee pollinator diversity and abundance in orchard and uncultivated habitats in the Okanagan Valley, British Columbia. *Canadian Entomologist* 119:735–745.
- Scott-Dupree, C.D., M. Winston, G. Hergert, S.C. Jay, D. Nelson, J. Gates, B. Termeer, and G. Otis, eds. 1995. *A Guide to Managing Bees for Crop Pollination*. Canadian Association of Professional Apiculturalists.

- Sears, M.K., R.L. Hellmich, D.E. Stanley-Horn, K.S. Oberhauser, J.M. Pleasants, H.R. Mattila, B.D. Siegfried, and G.P. Dively. 2001. Impact of *Bt* corn pollen on monarch butterfly populations: a risk assessment. *Proceedings of the National Academy of Sciences USA* 98:11937–11942.
- Seeley, T.D. 1985. *Honeybee Ecology*. Princeton: Princeton University Press. 201 pp.
- Seeley, T.D. 2003. Bees in the forest, still. *Bee Culture* 131:24–27.
- Sekita, N. 2001. Managing *Osmia cornifrons* to pollinate apples in Aomori Prefecture, Japan. *Acta Horticulturae* 561:303–307.
- SEMARNAT (Secretaría de Medio Ambiente y Recursos Naturales). 2002. Norma Oficial Mexicana NOM-059-ECOL-2001, Protección ambiental—Especies nativas de México de flora y fauna silvestres—Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio—Lista de especies en riesgo. *Diario Oficial*, March 6, 2002:1–56.
- Settele, J., V. Hammen, P. Hulme, U. Karlson, S. Klotz, M. Kotarac, W. Kunin, G. Marion, M. O'Connor, T. Petanidou, K. Peterson, S. Potts, H. Pritchard, P. Pysek, M. Rounsevell, J. Spangenberg, I. Steffan-Dewenter, M. Sykes, M. Vighi, M. Zobel, and I. Kühn. 2005. ALARM: Assessing large-scale environmental risks for biodiversity with tested methods. *Gaia* 14:69–72.
- Sheffield, C.S. 2006. Diversity and management of bees for the pollination of apple in the Annapolis Valley of Nova Scotia. Ph.D. thesis, University of Guelph, Canada.
- Shelton, A.M., and R. Roush. 1999. False reports and the ears of men. *Nature Biotechnology* 17:832.
- Shepherd, M.D. 2002. Making Room for Pollinators: How to Create Habitat for Pollinator Insects on Golf Courses. 2002. Far Hills, N.J.: U.S. Golf Association.
- Shepherd, M.D., and V.J. Tepedino. 2000. The birdies and the bees. *Green Section, Record* 38:17–21.
- Shepherd, M.D., D. Heagerty, and B. Baker. 2001. Environmental opportunity: pollinating bugs need homes. *Golf Course Management*. February:55–60.
- Shepherd, M.D., S.L. Buchmann, M. Vaughan, and S.H. Black. 2003. *Pollinator Conservation Handbook: A Guide to Understanding, Protecting, and Providing Habitat for Native Pollinator Insects*. The Xerces Society in Association with The Bee Works. Portland: The Xerces Society. 145 pp.
- Shepherd, M.D., D.M. Vaughan, and S.H. Black. eds. 2005. *Red List of Pollinator Insects of North America*. CD-ROM Version 1 (May 2005). Portland: The Xerces Society for Invertebrate Conservation. Available at: http://www.xerces.org/Pollinator_Red_List/index.htm.
- Sheppard, W.S. 1989a. A history of the introduction of honey bee races into the United States. I. *American Bee Journal* 129:617–619.
- Sheppard, W.S. 1989b. A history of the introduction of honey bee races into the United States. II. *American Bee Journal* 129:664–667.
- Sheppard, W.S. 2006. Breeding bees, mite resistance to pesticides and the limitations of bee research. *Bee Culture* 134:15–16.
- Sherman, P.W., E.A. Lacey, H.K. Reeve, and L. Keller. 1995. The eusociality continuum. *Behavioral Ecology* 6(11):102–108.
- Shimanuki, H. 1997. Bacteria. In: *Honey Bee Pests, Predators, and Diseases*, R.A. Morse and K. Flottum, eds., 3rd edition. Medina, Ohio: A. I. Root Company.
- Shimanuki, H., and D.A. Knox. 1994. Susceptibility of *Bacillus larvae* to Terramycin. *American Bee Journal* 134(2):125–126.
- Shimanuki, H., D.A. Knox, M. Delfinado-Baker, and P.J. Lima. 1983. National honey bee mite survey. *Apidologie* 14(4):329–332.
- Shimanuki, H., N.W. Calderone, and D.A. Knox. 1994. Parasitic mite syndrome: the symptoms. *American Bee Journal* 134:827–828.

- Shuler, R.E., T.H. Roulston, and G.E. Farris. 2005. Farming practices influence wild pollinator populations on squash and pumpkins. *Journal of Economic Entomology* 98:790–795.
- Shykoff, J.A., and P. Schmid-Hempel. 1991. Incidence and effects of four parasites in natural populations of bumble bees in Switzerland. *Apidologie* 22(2):117–125.
- SIAP (Sistema Integral de Información Agroalimentaria y Pesquera). 2005. Abeja: Población Apícola., Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación (SAGARPA). Available at: http://www.siap.sagarpa.gob.mx/ar_compec_pobgan.html. Accessed April 17, 2006.
- Sibley, D.A. 2000. *The Sibley Guide to Birds*. New York: Alfred A. Knopf.
- Simberloff, D.S., and E.O. Wilson. 1969. Experimental zoogeography of islands: the colonization of empty islands. *Ecology* 50:278–289.
- Simpson, R.D. 2002. Definitions of Biodiversity and Measures of Its Value. Discussion Paper 02-62. Washington: Resources for the Future.
- Simpson, R.D., R.A. Sedjo, and J.W. Reid. 1996. Valuing biodiversity for use in pharmaceutical research. *Journal of Political Economy* 104(1):163–185.
- Singer, R.B. 2003. Orchid pollination: recent developments from Brazil. *Lankesteriana* 7:111–114.
- Sinnot, E.W. 1946. *Botany Principles and Problems*. 4th edition. New York: McGraw-Hill. 726 pp.
- Slauson, L.A. 2000. Pollination biology of two chiropterophilous agaves in Arizona. *American Journal of Botany* 87:825–836.
- Slauson, L.A. 2001. Insights on the pollination biology of *Agave* (Agavaceae). *Haseltonia* 8:10–23.
- Smallidge, P.J., and D.J. Leopold. 1997. Vegetation management for the maintenance and conservation of butterfly habitats in temperate human-dominated landscapes. *Landscape and Urban Planning* 38(3–4):259–280.
- Smith, D.A. 1977. The first honeybees in America. *Bee World* 58:56.
- Snelling, R.R. 1983. Studies on North American bees of the genus *Hylaeus*: 6. An adventive Palearctic species in Southern California (Hymenoptera: Colletidae). *Bulletin of the Southern California Academy of Sciences* 82:12–16.
- Snow, A.A., and D.F. Whigham. 1989. Costs of flower and fruit production in *Tipularia discolor* (Orchidaceae). *Ecology* 70:1286–1293.
- Snyder, R.G. 1999. Southeastern United States Greenhouse Vegetable Growers Conference and Trade Show Proceedings. Available at: <http://nfrec-sv.ifas.ufl.edu/Reports%20HTML/proceedings.htm>. Accessed June 13, 2006.
- Snyder, R.G. 2006. Letter to potential exhibitors for the 16th annual Greenhouse Tomato Short Course. Available at: <http://www.msstate.edu/dept/cmrec/ExhibLetterWeb.pdf>.
- Soroka, J.J., D.W. Goerzen, K.C. Falk, and K.E. Bett. 2001. Alfalfa leafcutting bee (Hymenoptera: Megachilidae) pollination of oilseed rape (*Brassica napus* L.) under isolation tents for hybrid seed production. *Canadian Journal of Plant Science* 81(1):199–204. Ottawa: Agricultural Institute of Canada.
- Southwick, E.E., and L. Southwick, Jr. 1992. Estimating the economic value of honey bees (Hymenoptera: Apidae) as agricultural pollinators in the United States. *Journal of Economic Entomology* 85(3):621–633.
- Spivak, M., and D.L. Downey. 1998. Field assays for hygienic behaviour in honey bees (Hymenoptera: Apidae). *Journal of Economic Entomology* 91(1):64–70.
- Spivak, M., and M. Gilliam. 1998a. Hygienic behaviour of honey bees and its application for control of brood diseases and *Varroa*. Part I. Hygienic behaviour and resistance to American foulbrood. *Bee World* 79(3):124–134.
- Spivak, M., and M. Gilliam. 1998b. Hygienic behaviour of honey bees and its application for control of brood diseases and varroa. Part II. Studies on hygienic behaviour since the Rothenbuhler era. *Bee World* 79(4):169–186.

- Spivak, M., and G.S. Reuter. 1998. Performance of hygienic honey bee colonies in a commercial apiary. *Apidologie* 29:285–296.
- Spivak, M., G.S. Reuter, and M. Lamb. 1995. Frequency of hygienic behavior in naturally mated daughters of a hygienic breeder queen. *American Bee Journal* 135(12):830.
- Sprengel, C.K. 1793. *Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen* [The Secret of Nature in the Form and Fertilization of Flowers Discovered]. Berlin: Friedrich Vieweg der Ältere.
- Stang, M., P.G.L. Kinkhamer, and E. van der Meijden. 2006. Size constraints and flower abundance determine the number of interactions in a plant-flower visitor web. *Oikos* 112:111–121.
- Stanghellini, M.S., J.T. Ambrose, and J.R. Schultheis. 1996a. Establishing bumble bees as supplementary pollinators for honey bees for watermelon. *HortScience* 31(4):668.
- Stanghellini, M.S., J.T. Ambrose, and J.R. Schultheis. 1996b. Bumble bee: an alternative pollinator for cucumber. *HortScience* 31(5):746.
- Stanghellini, M.S., J.T. Ambrose, and J.R. Schultheis. 1997. The effects of honey bee and bumble bee pollination on fruit set and abortion of cucumber and watermelon. *American Bee Journal* 137:386–391.
- Stanley-Horn, D.E., G.P. Dively, R.L. Hellmich, H.R. Mattila, M.K. Sears, R. Rose, L.C. Jesse, J.E. Losey, J.J. Obrycki, and L. Lewis. 2001. Assessing the impact of Cry1Ab-expressing corn pollen on monarch butterfly larvae in field studies. *Proceedings of the National Academy of Sciences USA* 98:11931–11936.
- Stannard, L.J. 1957. The phylogeny and classification of the North American genera of the suborder Tubulifera (Thysanoptera). *Illinois Biological Monographs* 25:1–200.
- Stannard, L.J. 1968. The thrips, or Thysanoptera, of Illinois. *Bulletin of the Illinois Natural History Survey* 29:211–252.
- Statistics Canada. 2006. *Production and Value of Honey and Maple*. Catalogue No. 23-221-XIB. Ottawa: Statistics Canada. Available at: <http://www.statcan.ca/english/freepub/23-221-XIB/23-221-XIB2005000.pdf>.
- Stebbins, G.L. 1950. *Variation and Evolution in Plants*. New York: Columbia University Press.
- Stebbins, G.L. 1974. *Flowering Plants. Evolution above the Species Level*. Cambridge, Mass.: Harvard University Press.
- Stefanescu, C., J. Peñuelas, and I. Filell. 2003. Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Global Change Biology* 9(10):1494.
- Steffan-Dewenter, I. 2003. Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology* 17:1036–1044.
- Steffan-Dewenter, I., and T. Tschardtke. 1999. Effects of habitat isolation on pollinator communities and seed set. *Oecologia* 121:432–440.
- Steffan-Dewenter, I., U. Münzenberg, and T. Tschardtke. 2001. Pollination, seed set and seed predation on a landscape scale. *Proceedings of the Royal Society of London Series B* 268:1685–1690.
- Steffan-Dewenter, I., U. Munzenberg, C. Burger, C. Thies, and T. Tschardtke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83:1421–1432.
- Steffan-Dewenter, I., S.G. Potts, and L. Packer. 2005. Pollinator diversity and crop pollination services are at risk. *Trends in Ecology and Evolution* 20(12):651–652.
- Steffan-Dewenter, I., A.M. Klein, V. Gaebele, T. Alfert, and T. Tschardtke. 2006. Bee diversity and plant-pollinator interactions in fragmented landscapes. Pp. 387–410 in *Specialization and Generalization in Plant–Pollinator Interactions*, N.M. Waser and J. Ollerton, eds. Chicago: University of Chicago Press.

- Steiner K.E., and V.B. Whitehead. 1996. The consequences of specialization for pollination in a rare South African shrub, *Ixianthes retzioides* (Scrophulariaceae). *Plant Systematics and Evolution* 201:131–138.
- Stephanou, M., Y. Petropoulou, O. Georgiou, and Y. Manetas. 2000. Enhanced UV-B radiation, flower attributes and pollinator behaviour in *Cistus creticus*: a Mediterranean field study. *Plant Ecology* 147:165–171.
- Stephen, W.P. 2003. Solitary bees in North American agriculture: a perspective. Pp. 41–66 in *For Nonnative Crops, Whence Pollinators of the Future*, K. Strickler and J.H. Cane, eds. Proceedings, Entomological Society of America. Lanham, Md.: Thomas Say Publications in Entomology.
- Stephen, W.P., and B.L. Fichter. 1990a. Chalkbrood (*Ascospaera aggregata*) resistance in the leafcutting bee (*Megachile rotundata*). I. Challenge of selected lines. *Apidologie* 21(3):209–219.
- Stephen, W.P., and B.L. Fichter. 1990b. Chalkbrood (*Ascospaera aggregata*) resistance in the leafcutting bee (*Megachile rotundata*). II. Random matings of resistant lines to wild type. *Apidologie* 21(3):221–231.
- Stephen, W.P., and P.F. Torchio. 1961. Biological notes on the leaf-cutter bee, *Megachile* (Eutricharaea) *rotundata* (Fabricius). *Pan-Pacific Entomologist* 37:85–93.
- Stephen, W.P., G.E. Bohart, and P.F. Torchio. 1969. *The Biology and External Morphology of Bees*. Corvallis: Agricultural Experiment Station, Oregon State University.
- Stephen, W.P., J.D. Vandenberg, and B.L. Fichter. 1981. Etiology and epizootiology of chalkbrood in the leafcutting bee, *Megachile rotundata* (Fabricius), with notes on *Ascospaera* species. *Oregon State University Agricultural Experimentation Station Bulletin* 653.
- Stephenson, A.G. 1981. Toxic nectar deters nectar thieves of *Catalpa speciosa*. *American Midland Naturalist* 105:381–383.
- Stiles, F.G., and A.F. Skutch. 1989. *A Guide to the Birds of Costa Rica*. New York: Cornell University Press.
- Stoner, K.E., K.A.O. Salazar, R.C.R. Fernandez, and M. Quesada. 2003. Population dynamics, reproduction, and diet of the lesser long-nosed bat (*Leptonycteris curasoae*) in Jalisco, Mexico: implications for conservation. *Biodiversity and Conservation* 12:357–373.
- Stork, N.E. 1988. Insect diversity: Facts, fiction, and speculation. *Biological Journal of the Linnean Society* 35:321–337.
- Stork, N.E. 1997. Measuring global biodiversity and its decline. Pp. 41–68 in *Biodiversity II: Understanding and Protecting our Biological Resources*, M.L. Reaka-Kudla, D.E. Wilson, and E.O. Wilson, eds. Washington: Joseph Henry Press. 551 pp.
- Strickler, K., and J. Cane, eds. 2003. *For Nonnative Crops, Whence Pollinators of the Future?* Proceedings, Entomological Society of America. Lanham, Md.: Thomas Say Publications in Entomology. 204 pp.
- Stubbs, C.S., and F.A. Drummond. 1997a. Pollination of wild lowbush blueberry, *Vaccinium angustifolium* by the alfalfa leafcutting bee, *Megachile rotundata*. *Acta Horticulturae* (446):189–196.
- Stubbs, C.S., and F.A. Drummond. 1997b. Management of the alfalfa leafcutting bee, *Megachile rotundata* (Hymenoptera: Megachilidae), for pollination of wild lowbush blueberry. *Journal of the Kansas Entomological Society* 70(2):81–93.
- Stubbs, C.S., and F.A. Drummond. 2001. *Bees and Crop Pollination—Crisis, Crossroads, Conservation*. Proceedings, Entomological Society of America. Lanham, Md.: Thomas Say Publications in Entomology. 156 pp.
- Stubbs, C.S., F.A. Drummond, and E.A. Osgood. 1994. *Osmia ribifloris bidermannii* and *Megachile rotundata* (Hymenoptera: Megachilidae) introduced into the lowbush blueberry agroecosystem in Maine. *Journal of the Kansas Entomological Society* 67:173–185.
- Stubbs, C.S., F.A. Drummond, and S.L. Allard. 1997. Bee conservation and increasing *Osmia* spp. in Maine wild blueberry fields. *Northeastern Naturalist* 4:133–144.

- Sumner, D.A., and H. Boriss. 2006. Bee-economics and the leap in pollination fees. *Agricultural and Resource Economics Update* 9(Jan/Feb):9–11. Available at: http://www.agecon.ucdavis.edu/uploads/update_articles/v9n3_3.pdf.
- Swengel, A.B. 1990. Monitoring butterfly populations using the Fourth of July butterfly count. *American Midland Naturalist* 124:395–406.
- Swengel, A.B. 1995. Population fluctuations of the Monarch (*Danaus plexippus*) in the 4th of July butterfly count 1977–1994. *American Midland Naturalist* 134:205–221.
- Swingle, W.T. 1908. *The Fig in California*. Papers and discussions presented before the 34th and 35th Fruit-Growers' Convention, California. Sacramento: State Commission on Horticulture.
- Tang, J., J. Wice, V.G. Thomas, and P.G. Kevan. 2005. Assessment of the Capacity of Canadian Federal and Provincial Legislation to Conserve Native and Managed Pollinators. The International Network of Expertise for Sustainable Pollination, for the North American Pollinator Protection Campaign. Available at: <http://www.pollinator.org/Laws%20Affecting%20Pollinators-Canada.pdf>.
- Taséi, J.N., H. Sabik, L. Pirastru, E. Langiu, J.M. Blanche, J. Fournier, and J.P. Tagliani. 1994. Effects of sublethal doses of deltamethrin (Decis) on *Bombus terrestris*. *Journal of Apicultural Research* 33:129–135.
- Taséi, J.N., G. Ripault, and E. Rivault. 2001. Hazards of imidacloprid seed coating to *Bombus terrestris* (Hymenoptera: Apidae) when applied to sunflower. *Journal of Economic Entomology* 94(3):623–627.
- Taylor, O.R., Jr. 1977. The past and possible future spread of Africanized honeybees in the Americas. *Bee World* 58(1):19–30.
- Taylor, O.R., Jr. 2000. 40 years of tagging Monarch. *Watch Season 2000 Summary* 8:44–46.
- Téllez, G., and J. Ortega. 1999. *Musonycteris harrisoni*. *Mammalian Species* (American Society of Mammalogists) 622:1–3.
- Temeles, E.J., Y.B. Linhart, M. Masonjones, and H.D. Masonjones. 2002. The role of flower width in hummingbird bill length-flower length relationships. *Biotropica* 34:68–80.
- Tepedino, V.J. 1997. A comparison of the alfalfa leafcutting bee (*Megachile rotundata*) and the honey bee (*Apis mellifera*) as pollinators for hybrid carrot seed in field cages. Pp. 457–461 in *Proceedings of the 7th International Symposium on Pollination*, Lethbridge, Alberta, Canada, 23–28 June 1996, K.W. Richards, ed. Leiden, Netherlands: International Society for Horticultural Science.
- Tepedino, V.J., and H.S. Ginsberg. 2000. Report of the U.S. Department of Agriculture and U.S. Department of Interior Joint Workshop on Declining Pollinators, May 27–28, 1999, Logan, Utah. U.S. Geological Survey, Biological Resources Division, Information and Technology Report USGS/BRD/ITR-2000-0007, 9 pp.
- Tequila Aficionado. 2001. Tequila Sales Skyrocket; Agave Shortage Continue. Available at: <http://www.tequilaaficionado.com/article.php?sid=83>. Accessed February 24, 2001.
- Terry, I. 1997. Host selection, communication, and reproductive behaviour. Pp. 64–118 in *Thrips as Crop Pests*, T. Lewis, ed. London: CAB International.
- Terry, I. 2001. Thrips and weevils as dual, specialist pollinators of the Australian cycad *Macrozamia communis* (Zamiaceae). *International Journal of Plant Sciences* 162:1293–1305.
- Terzo, M., and F.J. Ortiz-Sanchez. 2004. Nuevos datos para las especies de ceratinini de España y Portugal, con una clave para su identificación (Hymenoptera, Apoidea, Xylocopinae). *Graellsia* 60(1):13–26.
- Terzo, M., and P. Rasmont. 2004. Biogéographie et systématique des abeilles rubicoles du genre *Ceratina* Latreille au Turkestan (Hymenoptera, Apoidea, Xylocopinae). *Annales de la Société Entomologique de France* 40(2):109–130.

- Tewksbury, J.J., D.J. Levey, N.M. Haddad, S. Sargent, J.L. Orrock, A. Weldon, B.J. Danielson, J. Brinkerhoff, E.I. Damschen, and P. Townsend. 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences USA* 99:12923–12926.
- Thien, L.B. 1974. Floral biology of Magnolia. *American Journal of Botany* 61:1037–1045.
- Thien, L.B., and V. Rico-Gray. 2004. Ant-orchid interactions. *Orchids* 73(8):606–617.
- Thien, L.B., and F. Utech. 1970. The mode of pollination in *Habenaria obtusata* (Orchidaceae). *American Journal of Botany* 57:1031–1035.
- Thien, L.B., E. Elgaard, M. Devall, S. Ellgaard, and R. Ramp. 1999. Population structure and reproductive biology of *Saururus cenuus* L. (Saururaceae). *Plant Species Biology* 9:47–55.
- Thomas, C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, M.F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A.S. van Jaarsveld, G.F. Midgley, L. Miles, M.A. Ortega-Huerta, A.T. Peterson, O.L. Phillips, and S.E. Williams. 2004. Extinction risk from climate change. *Nature* 427:145–148.
- Thomas, J.A., M.G. Telfer, D.B. Roy, C.D. Preston, J.J.D. Greenwood, J. Asher, R. Fox, R.T. Clarke, and J.H. Lawton. 2004. Comparative losses of british butterflies, birds, and plants and the global extinction crisis. *Science* 303:1879–1881.
- Thomas, M.C. 1998. Florida pest alert—the small hive beetle. *American Bee Journal* 138:565.
- Thompson, A.R. 2003. The issues facing the industry of the management of resistance in Europe. Pp. 695–702 in *The BCPC International Congress: Crop Science and Technology, Volumes 1 and 2 Proceedings of an International Congress held at the SECC, Glasgow, Scotland, UK, November 10–12, 2003*. Alton: British Crop Protection Council.
- Thompson, F.C. 1990. Biosystematic information: dipterists ride the third wave. Pp. 179–201 in *Systematics of the North American Insects and Arachnids: Status and Needs*, M. Kosztarab and C.W. Schaefer, eds. Virginia Agricultural Experiment Station Information series 90-1. Blacksburg: Virginia Polytechnic Institute and State University.
- Thompson, F.C., ed. 2006. Biosystematic Database of World Diptera. Available at: <http://www.diptera.org/names>. Accessed April 22, 2006.
- Thompson, H.M. 2001. Assessing the exposure and toxicity of pesticides to bumblebees (*Bombus* sp.). *Apidologie* 32:305–321.
- Thompson, J.N. 1982. *Interaction and Coevolution*. New York: Wiley and Sons. 179 pp.
- Thompson, J.N. 1994. *The Coevolutionary Process*. Chicago: University of Chicago Press. 387 pp.
- Thompson, J.N. 2005. *The Geographic Mosaic of Coevolution*. Chicago: University of Chicago Press.
- Thomson, D.M. 2004. Competitive interactions between the invasive European honey bee and native bumble bees. *Ecology* 85(2):458–470.
- Thomson, D.M. 2006. Detecting the effects of introduced species: a case study of competition between *Apis* and *Bombus*. *Oikos* 114(3):407–418.
- Thomson, J.D., and K. Goodell. 2001. Pollen removal and deposition by honeybee and bumblebee visitors to apple and almond flowers. *Journal of Applied Ecology* 38:1032–1044.
- Thomson, J.D., and B.A. Thomson. 1992. Pollen presentation and viability schedules in animal-pollinated plants: consequences for reproductive success. Pp. 1–24 in *Ecology and Evolution of Plant Reproduction: New Approaches*, R. Wyatt, ed. New York: Chapman and Hall.
- Thomson, J.D., R.C. Plowright, and G.R. Thaler. 1985. Matacil insecticide spraying, pollinator mortality, and plant fecundity in New Brunswick forests. *Canadian Journal of Botany* 63:2056–2061.

- Thorp, R.W. 1996. Resource overlap among native and introduced bees in California. Pp. 143–151 in *The Conservation of Bees*, A. Matheson, S.L. Buchmann, C. O'Toole, P. Westrich, and H. Williams, eds. London: Academic.
- Thorp, R.W. 2003. Bumble bees (Hymenoptera: Apidae): commercial use and environmental concerns. Pp. 21–40 in *For Nonnative Crops, Whence Pollinators of the Future?* K. Strickler and J.H. Cane, eds. Proceedings, Entomological Society of America. Lanham, Md.: Thomas Say Publications in Entomology.
- Thorp, R.W. 2005. *Bombus franklini* Frison, 1921 Franklin's bumble bee (Hymenoptera: Apidae: Apinae: Bombini). In *Red List of Pollinator Insects of North America*. CD-ROM Version 1, M.D. Shepherd, M.Vaughan, and S.H. Black, eds. Portland: The Xerces Society for Invertebrate Conservation.
- Thorp, R.W., and M.D. Shepherd. 2005. Species profile: subgenus *Bombus*. In *Red List of Pollinator Insects of North America*. CD-ROM Version 1, M.D. Shepherd, M.Vaughan, and S.H. Black, eds. Portland: Xerces Society for Invertebrate Conservation.
- Thorp, R.W., A.M. Wenner, and J.F. Barthell. 2000. Proceedings of the Fifth California Islands Symposium, D.R. Browne, K.L. Mitchell, and H.W. Chaney, eds. Washington: U.S. Department of the Interior, Mineral Management Service.
- Thorp, R.W., P.C. Schroeder, and C.S. Ferguson. 2003. Bumble bees: boisterous pollinators of native California flowers. *Fremontia* 30(3–4):26–31.
- Tilden, J.W. 1956. San Francisco's vanishing butterflies. *Lepidoptera News* 10:133–145.
- Ting, Z., Q. Wang, and Y. Jun. 2003. I: Advances in research of fluvalinate resistance in *Varroa destructor*: sodium channels involved. *Entomological Knowledge* 40(6):491–495.
- Toledo, V.M. 1977. Pollination of some rain forest plants by non-hovering birds in Veracruz, Mexico. *Biotropica* 9:262–267.
- Toledo, V.M., and H.M. Hernandez. 1979. *Erythrina oliviae*—New case of oriole pollination in Mexico. *Annals of the Missouri Botanical Garden* 66:503–511.
- Tonhasca, A., J.L. Blackmer, and G.S. Albuquerque. 2002. Abundance and diversity of euglossine bees in the fragmented landscape of the Brazilian Atlantic forest. *Biotropica* 34:416–422.
- Torchio, P.F. 1973. Relative toxicity of insecticides to the honey bee alkali bee and alfalfa leaf-cutting bee hymenoptera apidae halictidae megachilidae. *Journal of the Kansas Entomological Society* 46:446–453.
- Torchio, P.F. 1981a. Field experiments with *Osmia lignaria propinqua* Cresson as a pollinator in almond orchards. I. 1975 studies (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 54(4):815–823.
- Torchio, P.F. 1981b. Field experiments with *Osmia lignaria propinqua* Cresson as a pollinator in almond orchards. II. 1976 studies (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 54(4):824–836.
- Torchio, P.F. 1982. Field experiments with *Osmia lignaria propinqua* Cresson as a pollinator in almond orchards. III. 1977 studies (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 55(1):101–116.
- Torchio, P.F. 1990. Diversification of pollination strategies for U.S. crops. *Environmental Entomology* 19(6):1649–1656.
- Torchio, P.F. 2003. The development of *Osmia lignaria* Say (Hymenoptera: Megachilidae) as a managed pollinator of apple and almond crops: a case history. Pp. 67–84 in *For Nonnative Crops, Whence Pollinators of the Future?* K. Strickler and J.H. Cane, eds. Proceedings, Entomological Society of America. Lanham, Md.: Thomas Say Publications in Entomology.
- Torchio, P.F., and E. Asensio. 1985. The introduction of the European bee, *Osmia cornuta*, into the USA as a potential pollinator of orchard crops, and a comparison of its manageability with *Osmia lignaria propinqua* (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 58:42–52.

- Torchio, P.F., E. Asensio, and R.W. Thorp. 1987. Introduction of the European bee, *Osmia cornuta*, into California almond orchards (Hymenoptera: Megachilidae). *Environmental Entomology* 16:664–667.
- Torres, J.A., and R.R. Snelling. 1997. Biogeography of Puerto Rican ants: a non-equilibrium case. *Biodiversity Conservation* 6(8):1103–1121.
- Townsend, P.A., and D.J. Levey. 2005. An experimental test of whether habitat corridors affect pollen transfer. *Ecology* 86:466–475.
- Trejo, I., and R. Dirzo. 2000. Deforestation of seasonally dry tropical forest: a national and local analysis in Mexico. *Biological Conservation* 94:133–142.
- Tschapka, M., and O. von Helversen. 1999. Pollinators of syntopic *Marcgravia* species in Costa Rican lowland rain forest: bats and opossums. *Plant Biology* 1:382–388.
- Tscharntke, T., A. Gathmann, and I. Steffan-Dewenter. 1998. Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology* 35:708–719.
- Tscharntke, T., A.M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. *Ecology Letters* 8(8):857–874.
- Tudor, O., R.L.H. Dennis, J.N. Greatorex-Davies, and T.H. Sparks. 2004. Flower preferences of woodland butterflies in the UK: nectaring specialists are species of conservation concern. *Biological Conservation* 119:397–403.
- Turner, W.R. 2003. Citywide biological monitoring as a tool for ecology and conservation in urban landscapes: the case of the Tucson Bird Count. *Landscape and Urban Planning* 65:149–166.
- Turncock, V.J., P.G. Kevan, T.M. Lavery, and L. Dumouchel. Abundance of species of bumble bees (Hymenoptera, Apoidea, Bombinae) in fields of Canola, *Brassica rapa* L, in Manitoba, an 8-year record. In preparation.
- Turner, W.R., T. Nakamura, and M. Dinetti. 2004. Global urbanization and the separation of humans from nature. *Bioscience* 54:585–590.
- Tuttle, M.D. 2000. Where the bats are—part III: caves, cliffs, and rock crevices. *Bat Magazine* 18(1):6–11.
- Ullman, D.E., J.L. Sherwood, and T.G. German. 1997. Thrips as vectors of plant pathogens. Pp. 539–565 in *Thrips as Crop Pests*, T.L. Lewis, ed. London: CAB International.
- UK Department of Environment, Food and Rural Affairs. 2002. ERDP Scheme Introduction. Available at: <http://www.defra.gov.uk/erdp.schemes/default.htm>. Accessed August 23, 2006.
- USDA-AMS (U.S. Department of Agriculture Agricultural Marketing Service). 2004. Honey Research, Promotion, and Consumer Information Order. U.S. Department of Agriculture. Available at: <http://www.ams.usda.gov/fv/rphoney.html>. Accessed March 10, 2006.
- USDA-AMS. 2005. How to Request a National Research and Promotion Program. Livestock and Seed Program, Agricultural Marketing Service, U.S. Department of Agriculture. Available at: <http://www.ams.usda.gov/lsg/mpb/generic/generic.htm>. Accessed December 30, 2005.
- USDA-APHIS (U.S. Department of Agriculture Animal and Plant Health Inspection Service). 2002. Risk Assessment: Importation of Adult Queens, Package Bees and Germplasm of Honey Bees, *Apis mellifera* L., from Australia. U.S. Department of Agriculture, APHIS. Available at: http://www.aphis.usda.gov/ppq/prahoneybees/aushbee_pra.html. Accessed December 30, 2005.
- USDA-APHIS. 2004. Animal and Plant Health Inspection Service: Bees and Related Articles, Final Rule. *Federal Register* 7 CFR Parts 319 and 322, 69(203):61735–61755.
- USDA-ERS (U.S. Department of Agriculture Economic Research Service). 2004. Fruit and Tree Nuts Outlook. U.S. Department of Agriculture. Available at: <http://www.ers.usda.gov/Briefing/FruitandTreeNuts/fruitnutpdf/Figs.pdf>. Accessed May 16, 2006.

- USDA-FSA (U.S. Department of Agriculture Farm Service Agency). 2006. Conservation Reserve Program. U.S. Department of Agriculture. Available at: <http://www.fsa.usda.gov/dafp/cepd/crp.htm>. Accessed March 10, 2006.
- USDA-NASS (U.S. Department of Agriculture National Agricultural Statistics Service). 1995. Honey: Final estimates for 1986–1992. Statistical Bulletin No. 912, March. Washington: U.S. Department of Agriculture.
- USDA-NASS. 1999. Honey: Final estimates for 1993–1997. Statistical Bulletin No. 956, February. Washington: U.S. Department of Agriculture.
- USDA-NASS. 2004a. 2002 Census of Agriculture: United States Summary and State Data. AC-02-A-51 (June). Washington: U.S. Department of Agriculture. Available at: <http://www.nass.usda.gov/census/census02/volume1/us/USVolume104.pdf>. Accessed March 19, 2006.
- USDA-NASS. 2004b. Honey: Final estimates for 1998–2002. Statistical Bulletin No. 992. April. Washington: U.S. Department of Agriculture.
- USDA-NASS. 2005. Honey. Washington: U.S. Department of Agriculture. Available at: <http://usda.mannlib.cornell.edu/reports/nassr/other/zho-bb/hony0205.pdf>. Accessed February 28, 2005.
- USDA-NASS. 2006a. Honey. Washington: U.S. Department of Agriculture.
- USDA-NASS. 2006b. Crop Values: 2005 Summary. Washington: U.S. Department of Agriculture.
- USDA-NRCS (U.S. Department of Agriculture Natural Resources Conservation Service). 2004. Habitat development for pollinator insects. Biology Technical Note No. MT-20. Washington: U.S. Department of Agriculture.
- USDA-NRCS. 2006a. Native, culturally significant plants. Conservation Security Program Enhancement Activity Job Sheet. Plant Management EPL 40. Washington: U.S. Department of Agriculture. Available at: http://www.pa.nrcs.usda.gov/technical/Jobsheets/EPL40_Native_Culturally_Significant_Plants.pdf. Accessed April 5, 2006.
- USDA-NRCS. 2006b. Nectar corridors. Conservation Security Program Enhancement Activity Job Sheet. Plant Management EPL 41. Washington: U.S. Department of Agriculture. Available at: http://www.pa.nrcs.usda.gov/technical/Jobsheets/EPL41_Nectar_Corridors.pdf. Accessed April 5, 2006.
- USFWS (U.S. Fish and Wildlife Service). 1988. Endangered and Threatened Wildlife and Plants; Determination of Endangered Status for Two Long-nosed Bats. Federal Register 53:38456–38460. U.S. Department of the Interior.
- USFWS. 1994. Endangered and Threatened Wildlife and Plants. August 20, 1994. 50 CFR 17.11 and 17.12. U.S. Department of the Interior.
- USFWS. 2006. USFWS Threatened and Endangered Species System. U.S. Department of the Interior. Available at: <http://ecos.fws.gov>. Accessed September 12, 2006.
- Valenzuela-Zapata, A.G. 1994. El agave tequilero: Su cultivo e industrialización. Guadalajara, Mexico: Editorial Agata.
- Valenzuela-Zapata, A.G., and G.P. Nabhan. 2004. Tequila: A Natural and Cultural History. Tucson: University of Arizona Press.
- Valiente-Banuet, A. 2002. Vulnerability of pollination systems of columnar cacti of Mexico. *Revista Chilena de Historia Natural* 75(1):99–104.
- Valiente-Banuet, A., M.C. Arizmendi, A. Rojas-Martínez, and L. Domínguez-Canseco. 1996. Ecological relationships between columnar cacti and nectar feeding bats in Mexico. *Journal of Tropical Ecology* 12:103–119.
- Vamosi, J.C., T.M. Knight, J. Streets, S.J. Mazer, M. Burd, and T.-L. Ashman. 2006. Pollination decays in biodiversity hotspots. *Proceedings of the National Academy of Sciences* 103:956–961.
- Van der Cingel, N.A. 2001. *An Atlas of Orchid Pollination: America, Africa, Asia and Australia*. Rotterdam, Holland: A.A. Balkana.

- van der Pijl, L. 1982. Principles of Dispersal in Higher Plants. Berlin: Springer-Verlag. 214 pp.
- van Heemert, C., A. de Ruijter, J. van den Eijnde, and J. van der Steen. 1990. Year round production of bumble bee colonies for crop pollination. *Bee World* 71(2):54–56.
- Vance, M.D., L. Fahrig, and C.H. Flather. 2003. Effect of reproductive rate on minimum habitat requirements of forest-breeding birds. *Ecology* 84:2643–2653.
- Vance, N.C., P. Bernhardt, and R.M. Edens. 2004. Pollination and seed production in *Xerophyllum tenax* (Melanthiaceae) in the Cascade Range of Central Oregon. *American Journal of Botany* 91:2060–2068.
- Vandenberg, J.D., and W.P. Stephen. 1983. Pathogenesis of chalkbrood in the alfalfa leafcutting bee, *Megachile rotundata*. *Apidologie* 14(4):333–341.
- Vaughan, M., M. Shepard, C. Kremen, and S.H. Black. 2004. Farming for Bees: Guidelines for Providing Native Bee Habitat on Farms. Portland: The Xerces Society for Invertebrate Conservation.
- Vazquez, D.P., and M.A. Aizen. 2004. Asymmetric specialization: a pervasive feature of plant-pollinator interactions. *Ecology* 85:1251–1257.
- Velthuis, H.H.W. 2002. The historical background of the domestication of the bumble-bee, *Bombus terrestris*, and its introduction in agriculture. Pp. 177–184 in *Pollinating Bees—The Conservation Link Between Agriculture and Nature*, P. Kevan and V.L. Imperatriz Fonseca, eds. Brazil: Ministry of Environment.
- Villanueva-Gutierrez, R., D.W. Roubik, and W. Colli-Ucan. 2005. Extinction of *Melipona beecheii* and traditional beekeeping in the Yucatan peninsula. *Bee World* 86(2):35–41.
- Vinson, S.B., G.W. Frankie, and J. Barthell. 1993. Threats to the diversity of solitary bees in a neotropical dry forest in Central America. Pp. 53–82 in *Hymenoptera and Biodiversity*, J. LaSalle and I.D. Gauld, eds. Oxon: CAB International.
- Visscher, P.K., and T.D. Seeley. 1982. Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* 63:1790–1801.
- Vogel, S. 1969. Chiropterophilie in der neotropischen Flora. *Neue Mitteilungen II. Flora (B)* 158:185–222.
- von Frisch, K. 1967. *Tanzsprache und Orientierung der Bienen* [The Dance Language and Orientation of Bees]. Cambridge, Mass.: Harvard University Press.
- von Helversen, O., and Y. Winter. 2003. Glossophagine bats and their flowers: cost and benefit for plant and pollinator. Pp. 346–397 in *Bat Ecology*, T.H. Kunz and M.B. Fenton, eds. Chicago: University of Chicago Press.
- von Helversen, O., L. Winkler, and H.J. Bestmann. 2000. Sulphur-containing “perfumes” attract flower-visiting bats. *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology* 186:143–153.
- Walker-Simmons, M.K. 2003. New USDA-ARS research in biotechnology risk assessment. Pp. 95–99 in *NABC Report 15: Biotechnology: Science and Society at a Crossroad*, A. Eaglesham, S. Ristow, and R.W.F. Hardy, eds. Ithaca: National Agricultural Biotechnology Council.
- WallisdeVries, M.F., J.P. Bakker, and S.E. Van Wieren. 1998. *Grazing and Conservation*. Dordrecht, Boston, London: Kluwer Academic Publishers.
- WallisDeVries, M.F., P. Poschlod, and J.H. Willems, 2002. Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biology Conservation* 104:265–273.
- Walters, C.J., and C.S. Holling. 1990. Large-scale management experiments and learning by doing. *Ecology* 71(6):2060–2068.
- Walther, G.R. 2004. Plants in a warmer world. *Perspectives in Plant Ecology, Evolution and Systematics* 6:169–185.

- Walton, R.K., L.P. Brower, and A.K. Davis. 2005. Long-term monitoring and fall migration patterns of the Monarch butterfly in Cape May, New Jersey. *Annals of the Entomological Society of America* 98:682–689.
- Wang, R.W., Z.Q. Liu, K. Dong, P.J. Elzen, J. Pettis, and Z.Y. Huang. 2002. Association of novel mutations in a sodium channel gene with fluralinate resistance in the mite, *Varroa destructor*. *Journal of Apicultural Research* 41(1–2):17–25.
- Ward, M., and S.D. Johnson. 2005. Pollen limitation and demographic structure in small fragmented populations of *Brunsvigia radulosa* (Amaryllidaceae). *Oikos* 108(2):253.
- Warren, M.S., J.K. Hill, J.A. Thomas, J. Asher, R. Fox, B. Huntley, D.B. Roy, M.G. Telfer, S. Jeffcoate, P. Harding, G. Jeffcoate, S.G. Willis, J.N. Greatorex-Davies, D. Moss, and C.D. Thomas. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414:65–69.
- Waser, N.M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* 59:934–944.
- Waser, N.M. 1979. Pollinator availability as a determinant of flowering time in ocotillo (*Fouquieria splendens*). *Journal Oecologia* 39(1):107–121.
- Waser, N.M., and J. Ollerton, eds. 2006. *Plant-Pollinator Interactions: From Specialization to Generalization*. Chicago: University of Chicago Press. 488 pp.
- Waser, N.M., L. Chittka, M.V. Price, N.M. Williams, and J. Ollerton. 1996. Generalization in pollination systems, and why it matters. *Ecology* 77:1043–1060.
- Watanabe, M.E. 1994. Pollination worries rise as honey bees decline. *Science* 265:1170.
- Watson, L., and M.J. Dallwitz. 1992. *The Families of Flowering Plants: Descriptions, Illustrations, Identification, and Information Retrieval*. Version: June 2, 2006. <http://delta-intkey.com>.
- Wei, S.G., R. Wang, M.J. Smirle, and H.L. Xu. 2002. Release of *Osmia excavata* and *Osmia jacoti* (Hymenoptera: Megachilidae) for apple pollination. *Canadian Entomologist* 134(3):369–380.
- Weiblen, G.D. 2002. How to be a fig wasp. *Annual Review of Entomology* 47:299–330.
- Weibull, A.-Ch., Ö. Östman, and Å. Granqvist. 2003. Species richness in agro-ecosystems: the effect of landscape, habitat and farm management. *Biodiversity and Conservation* 12:1335–1355.
- Weller, S.G. 1994. The relationship of rarity to plant reproductive biology. Pp. 90–117 in *Restoration of Endangered Species. Conceptual Issues, Planning and Implementation*, M.L. Bowles and C.J. Whelan, eds. Cambridge, Mass.: Cambridge University Press.
- Westphal, C., I. Steffan-Dewenter, and T. Tscharntke. 2003. Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters* 6:961–965.
- Westrich, P. 1989. Pp. 381–390 in *Die Wildbienen Baden Württembergs*. Stuttgart: Eugen Ulmer.
- Westrich, P. 1990. Pp. 432–972 in *Die Wildbienen Baden-Württembergs. Vol. 2*. Stuttgart: Ulmer Verlag.
- Westrich, P. 1996. Habitat requirements of central European bees and the problems of partial habitats. Pp. 1–16 in *The Conservation of Bees*, A. Matheson, S.L. Buchmann, C. O'Toole, P. Westrich, and I.H. Williams, eds. London: Academic Press.
- White, G.F. 1920. American foulbrood. *US Department of Agriculture Bulletin* 809:46.
- White, G.M., D.H. Boshier, and W. Powell. 2002. Increased pollen flow counteracts fragmentation in a tropical dry forest: an example from *Swietenia humilis* Zuccarini. *Proceedings of the National Academy of Sciences USA* 99:2038–2042.
- Whittington, R., M.L. Winston, C. Tucker, and A.L. Parachnowitsch. 2004. Plant-species identity of pollen collected by bumblebees placed in greenhouses for tomato pollination. *Canadian Journal of Plant Science* 84:599–602.

- Wilkinson, G.S., and T.H. Fleming. 1996. Migration and evolution of lesser long-nosed bats *Leptonycteris curasoae*, inferred from mitochondrial DNA. *Molecular Ecology* 5:329–339.
- Willett, G.S., and W.J. Gary. 1992. Alfalfa seed enterprise budget Walla Walla County, Washington. Washington State University Cooperative Extension EB 1375. 13 pp.
- Williams, C.G., Y. Zhou, and S.E. Hall. 2001. A chromosomal region promoting outcrossing in a conifer. *Genetics* 159:1283–1289.
- Williams, N., and C. Kremen. Forthcoming (in press). The importance of local habitat, landscape composition and connectivity for population persistence of a solitary bee, *Osmia lignaria*, in a mosaic agricultural landscape. *Ecological Applications*.
- Williams, N.M., R.L. Minckley, and F.A. Silveira. 2001. Variation in native bee faunas and its implications for detecting community changes. *Conservation Ecology* 5:7.
- Williams, P. 1998. An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini). *Bulletin of the Natural History Museum, London (Entomology)* 67(1):79–152.
- Williams, T.A., and M.T. Abberton. 2004. Earlier flowering between 1962 and 2002 in agricultural varieties of white clover. *Oecologia* 138(1):122–126.
- Williamson, M.S., J.A. Anstead, G.J. Devine, A.L. Devonshire, L.M. Field, S.P. Foster, G.D. Moores, and I. Denholm. 2003. Insecticide resistance: from science to practice. Pp. 681–688 in BCPC International Congress: Crop Science and Technology, Volumes 1 and 2. Proceedings of an international congress held at the SECC, Glasgow, Scotland, UK, November 10–12, 2003.
- Wilson, D.E., D.V. Lanning, and R.A. Medellin. 1985. Bats from Northeastern Mexico, with a Checklist of Species. Washington: U.S. Fish and Wildlife Service, Museum Section. 30 pp.
- Wilson, E.O. 1971. *The Insect Societies*. Cambridge: Belknap.
- Wilson, E.O. 2003. The encyclopedia of life. *Trends in Ecology and Evolution* 18:2:77–80.
- Wilson, E.O., and B. Hölldobler. 2005. Eusociality: origin and consequences. *Proceedings of the National Academy of Sciences USA* 102(38):13367–13371.
- Wilson, R., D. Gutiérrez, J. Gutiérrez, D. Martínez, R. Agudo, and V.J. Monserrat. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters* 8(11):1138.
- Wilson, W.T. 1970. Inoculation of the pupal honeybee with spores of *Bacillus* larvae. *Journal of Apicultural Research* 9:33–37.
- Wilson, W.T., and A.M. Collins. 1993. Formic acid or amitraz for spring or fall treatment of *Acarapis woodi*. *American Bee Journal* 133(12):871.
- Wilson, W.T., J.R. Elliott, and J.D. Hitchcock. 1973. Treatment of American foulbrood with antibiotic extender patties and antibiotic paper packs. *American Bee Journal* 113:341–344.
- Wilson, W.T., J.S. Pettis, and A.M. Collins. 1989. Efficacy of different isomers of menthol against the honey bee tracheal mite. *American Bee Journal* 129:826.
- Wilson, W.T., R.L. Cox, J.O. Moffett, and M. Ellis. 1990. Improved survival of honey bee (*Apis mellifera* L.) colonies from long-term suppression of tracheal mites (*Acarapis woodi* Rennie) with menthol. *Bee Science* 1:48–54.
- Winfrey, R., T. Griswold, and C. Kremen. 2007. Effect of human disturbance on bee communities in a forested ecosystem. *Conservation Biology* 21:213–223.
- Winston, M.L. 1979. Intra-colony demography and reproductive rate of the Africanized honeybee in South America. *Behavioral Ecology and Sociobiology* 4(3):279–292.
- Winston, M.L. 1987. *Biology of the Honey Bee*. Cambridge, Mass.: Harvard University Press. 281 pp.
- Winston, M.L. 1992. *Killer Bees. The Africanized Honey Bee in the Americas*. Cambridge, Mass.: Harvard University Press. xiii + 162 pp.

- Winston, M.L., G.W. Otis, and O.R. Taylor, Jr. 1979. Absconding behaviour of the Africanized honeybee in South America. *Journal of Apicultural Research* 18(2):85–94.
- Winston, M.L., J.A. Dropkin, and O.R. Taylor, Jr. 1981. Demography and life history characteristics of two honey bee races (*Apis mellifera*). *Oecologia* 48:407–413.
- Winston, M.L., O.R. Taylor, Jr., and G.W. Otis. 1983. Some differences between temperate European and tropical African and South American honeybees. *Bee World* 64(1):12–21.
- Winter, K., L. Adams, R. Thorp, D. Inouye, L. Day, J. Ascher, and S. Buchmann. 2006. Importation of Non-native Bumble Bees into North America: Potential Consequences of using *Bombus terrestris* and other Non-native Bumble Bees for Greenhouse Crop Pollination in Canada, Mexico, and the United States. White Paper of the North American Pollinator Protection Campaign. Available at: http://www.nappc.org/WhitePaper-news_release_FINAL.pdf.
- Winter, Y., and O. von Helversen. 2001. Bats as pollinators: foraging energetics and floral adaptations. Pp. 148–170 in *Cognitive Ecology of Pollination*, L. Chittka and J.D. Thomson, eds. Cambridge: Cambridge University Press.
- Wolda, H. 1988. Insect seasonality: why? *Annual Review of Ecology and Systematics* 19:1–18.
- Wraight, C.L., A.R. Zangerl, M.J. Carroll, and M.R. Berenbaum. 2000. Absence of toxicity of *Bacillus thuringiensis* pollen to black swallowtails under field conditions. *Proceedings of the National Academy of Sciences USA* 97(14):7700–7703.
- Wu, J.Q., B.D. Siegfried, and M.D. Ellis. 2003. An investigation of the metabolic detoxification of fluralinate in *Varroa destructor* Anderson and Truemann. *Resistant Pest Management Newsletter* 13(1):70–75.
- Wyatt, R. 1981. Ant-pollination of the granite outcrop endemic *Diamorpha smallii* (Crassulaceae). *American Journal of Botany* 68:1212–1217.
- Wyatt, R., and A. Stoneburner. 1981. Patterns of ant-mediated pollen dispersal in *Diamorpha smallii* (Crassulaceae). *Systematic Botany* 6:1–7.
- Young, A.M. 1981. The ineffectiveness of the stingless bee *Trigona-Jaty* (Hymenoptera, Apidae, Meliponinae) as a pollinator of cocoa (*Theobroma-Cacao* L.). *Journal of Applied Ecology* 18(1):149–155.
- Young, A.M. 1982. Effects of shade cover and availability of midge breeding sites on pollinating midge populations and fruit-set in 2 cocoa farms. *Journal of Applied Ecology* 19(1):47–63.
- Young, A.M. 1985. Pollen-collecting by stingless bees on cacao flowers. *Experientia* 41(6):760–762.
- Young, A.M. 1986. Distribution and abundance of Diptera in flypaper traps at *Theobroma-Cacao* L (Sterculiaceae) flowers in Costa Rican cacao plantations. *Journal of the Kansas Entomological Society* 59(4):580–587.
- Young, A.M. 1994. *The Chocolate Tree: A Natural History of Cacao*. Washington: Smithsonian Institution Press.
- Yurlina, M.E. 1998. Bee mutualists and plant reproduction in urban woodland restorations. Ph.D. thesis, Rutgers University, New Brunswick, New Jersey.
- Zangerl, A.R., D. McKenna, C.L. Wraight, M. Carroll, P. Ficarello, R. Warner, and M.R. Berenbaum. 2001. Effects of exposure to event 176 *Bacillus thuringiensis* corn pollen on monarch and black swallowtail caterpillars under field conditions. *Proceedings of the National Academy of Sciences USA* 98:11908–11912.
- Zavaleta, E.S., R.J. Hobbs, and H.A. Mooney. 2001. Viewing invasive species removal in a whole ecosystem context. *Trends in Ecology and Evolution* 16:454–459.
- Zayed, A., and L. Packer. 2001. High levels of diploid male production in a primitively eusocial bee (Hymenoptera: Halictidae). *Heredity* 87:631–636.

- Zayed, A., and L. Packer. 2005. Complementary sex determination substantially increases extinction proneness of haplodiploid populations. *Proceedings of the National Academy of Sciences USA* 102:10742–10746.
- Zayed, A., D.W. Roubik, and L. Packer. 2004. Use of diploid male frequency data as an indicator of pollinator decline. *Proceedings of the Royal Society of London Series B—Biological Sciences* 271:S9–S12.
- Zedler, J.B., and J.C. Callaway. 1999. Tracking wetland restoration: Do mitigation sites follow desired trajectories? *Restoration Ecology* 7(1):69–73.
- Zimmerman, M., and G.H. Pyke. 1988. Reproduction in *Polemonium*: assessing the factors limiting seed set. *American Naturalist* 131:732–738.

Appendixes

Status of Pollinators in North America
<http://www.nap.edu/catalog/11761.html>

A

Committee Biographies

May Berenbaum (*Chair*) is Swanlund Professor and head of the Department of Entomology at the University of Illinois, Urbana-Champaign. Dr. Berenbaum obtained her Ph.D. in ecology and evolutionary biology from Cornell University in 1980 and joined the University of Illinois faculty shortly thereafter; she currently holds affiliate appointments in the Department of Plant Biology, the Department of Natural Resources and Environmental Sciences, and the Program in Ecology and Evolutionary Biology, and at the Center for Ecological Entomology at the Illinois Natural History Survey. Her primary research is on chemical mediation of interactions between plants and herbivorous insects, and her work ranges from the molecular to the community level. Dr. Berenbaum is a member of the National Academy of Sciences (NAS) and a fellow of several scientific societies, including the American Academy of Arts and Sciences. Her service to the National Academies has included two-terms as chair of the Board on Agriculture and Natural Resources, member of the NAS Council, and member of the National Research Council Report Review Committee. Dr. Berenbaum serves on several advisory boards and is currently president of the Board of Directors of the Xerces Society, an organization dedicated to the conservation of invertebrate animals.

Peter Bernhardt is a professor in the Department of Biology at St. Louis University and an associate of the Missouri Botanical Garden and the Royal Botanic Garden of Sydney. He received his Ph.D. in botany from the School of Botany at the University of Melbourne, Victoria, Australia. Since 1976, Dr. Bernhardt has done field work in the ecology of animal-pollinated angio-

sperms in relation to the compatibility (SI) systems. In North America, Dr. Bernhardt's studies have included work on insect-pollinated *Erythronium*, *Hepatica*, *Tolmeia*, *Penstemon*, and *Xerophyllum* spp. His laboratory is under contract with the U.S. Department of Agriculture Forest Services (Corvallis, Oregon) to study the pollination of three *Potentilla* species, *Paeonia brownie*, and *Cypripedium montanum*.

Stephen Buchmann is an adjunct professor of entomology and a research associate at the Arizona-Sonora Desert Museum and in the Department of Ecology and Evolutionary Biology at the University of Arizona. He is president and cofounder of The Bee Works, LLC, an environmental consulting company in Tucson. For 21 years, Dr. Buchmann was a research entomologist with the Carl Hayden Bee Research Center of the U.S. Department of Agriculture Agricultural Research Service. His research is on conservation biology, pollination ecology, bee nesting, mating biology and chemical ecology, "buzz pollination" of crops, and the oil-harvesting centridine bees of the New World tropics. He is the author of more than 150 scientific publications and of 8 books, including *The Forgotten Pollinators* published in 1996 with Dr. Gary Nabhan, and *Pollinators of the Sonoran Desert*, *Pollinator Conservation Handbook*, and *Letters from the Hive*. His first children's book is *The Bee Tree* (Cinco Puntos Press). With Gary Nabhan, he cofounded and directed the trinational Forgotten Pollinators Campaign from the Arizona-Sonora Desert Museum. Dr. Buchmann is a research associate in entomology with the American Museum of Natural History in New York City. He is a fellow of the Linnean Society of London. He serves on the steering committee of the North American Pollinator Protection Campaign and as its research chair. Dr. Buchmann routinely works with natural history film-makers and was associate producer of the 2001 "Pollinators in Peril" television documentary, produced by Turner Original Productions and the National Wildlife Federation.

Nicholas W. Calderone is director of the Cornell University Dyce Laboratory for Honey Bee Studies. He received his M.S. and Ph.D. from the Ohio State University. He currently has responsibilities in research, teaching, and extension, and he does work on methods for controlling parasites and pathogens of honey bees. His research concerns the development of Africanized-free honey bees that are resistant to parasitic mites and honey bee pathogens. He spent 7 years with the U.S. Department of Agriculture Agricultural Research Service's Bee Research Laboratory in Beltsville, Maryland where he focused on the biology of *Varroa destructor* and on the use of integrated pest management to control parasitic mites in honey bees. Dr. Calderone is the author of more than 40 peer-reviewed research papers and more than 30

extension articles on honey bee management. In 2000, he was coauthor of an article on the value of honey bee pollination to agricultural production in the United States. He also has developed a master beekeeper program that serves beekeepers in the northeastern United States.

Paul Goldstein is the assistant curator of Lepidoptera at the McGuire Center for Lepidoptera and Biodiversity of the Florida Museum of Natural History in Gainesville. Before moving to Florida, Dr. Goldstein was curator in the Division of Insects at the Field Museum of Natural History in Chicago, Illinois, where he presided over the Lepidoptera collection and served as a principal investigator in the Pritzker Laboratory for Molecular Systematics. Dr. Goldstein's research has focused on the evolution of host plant associations in herbivorous insects, particularly moths, and on conservation genetics and invertebrate conservation and monitoring programs in prairies, and in pitch pine and scrub oak barrens, among other unusual plant communities. Since 1986, Dr. Goldstein has devoted many of his conservation efforts to the Massachusetts coastline and its offshore islands, where he works on the conservation genetics of the northeastern beach tiger beetle, the reintroduction of the imperial moth, and the use of assemblages of threatened moths and butterflies for landscape-level conservation.

David W. Inouye is a professor in the Department of Biology at the University of Maryland, College Park. He was an undergraduate at Swarthmore College, and he received his Ph.D. in zoology from the University of North Carolina. He directs the graduate program in sustainable development and conservation biology at the University of Maryland and teaches courses in ecology and conservation biology. From 1988 to 1990, he was director of the University of Colorado's Mountain Research Station. Dr. Inouye has conducted field research at the Rocky Mountain Biological Laboratory (Colorado) since 1971, where he has studied resource partitioning in bumble bees, pollination biology, plant demography, and ant-plant mutualisms. His current work is on long-term studies of variation in the phenology and abundance of flowering by wildflowers—to identify the effects of environmental variables and climate change on flowering and to identify the consequences for consumers. He also has done research on pollination biology in the Snowy Mountains in Australia and in Panama. His field work has taken him to South Africa, Austria, and Costa Rica. Dr. Inouye is coauthor of the book *Techniques for Pollination Biologists*. He is a member of the Steering Committee of the North American Pollinator Protection Campaign, a member of the Task Force on Declining Pollination Services, of the Species Survival Commission of the IUCN (The World Conservation Union), and secretary of the Governing Board of the Ecological Society of America.

Peter Kevan is a professor of environmental biology and botany at the University of Guelph, Ontario, Canada. His experience in pollination started with work in the Canadian High Arctic. Since receiving his doctorate in 1970, Dr. Kevan has worked on pollination ecology in Asia, the Americas, Africa, Australia, and Europe. He also has worked extensively on natural, agricultural, plantation, and forest pollination problems, with special emphasis on practical and conservation issues. His research in the 1970s on the demise of pollinators caused by insecticides in New Brunswick, Canada, stimulated serious consideration of the consequences of pesticide use in forestry. He is chair of the Task Force on Declining Pollination of the IUCN (The World Conservation Union), he is actively involved in pollination initiatives arising from the Convention on Biological Diversity, and he is a member of the Steering Committee for the North American Pollinator Protection Campaign.

Claire Kremen is an assistant professor in the Department of Environmental Science, Policy, and Management at the University of California, Berkeley, and an associate conservationist with the Wildlife Conservation Society. She received her Ph.D. in zoology from Duke University and her B.Sc. in biology from Stanford University. Her current work is on the use of biological, social, and economic data to develop conservation plans that benefit people and the environment. She has studied an array of topics in conservation biology, including the economics and ecology of ecosystem services, sustainable forestry, the ecology and biogeography of tropical butterflies, the population biology of lemurs, and ecological monitoring. Her work reaches from theory to practice and includes hands-on conservation action. From 1993 to 1997, she designed and helped to establish Madagascar's largest National Park on the Masoala Peninsula. Her current research examines the functional links between the spatial distribution of wildlands, the composition of wild bee communities, farm management practices, and the delivery of pollination services for agriculture in California and New Jersey. She is leading a National Center for Ecological Analysis and Synthesis working group that uses models and meta-analysis to identify ways to restore pollination services in degraded landscapes. She also is working with organizations in Madagascar to establish a national conservation-planning tool by accumulating data on species occurrences, developing predictive models of species distributions, and conducting conservation analyses. She is a scientific advisor for several conservation organizations and she sits on the editorial board of *Conservation Biology*. She is a 2001 recipient of the McDonnell 21st Century Research Award.

Rodrigo A. Medellín is director of the Institute of Ecology at the National Autonomous University of Mexico. He is also an adjunct professor at

Columbia University in New York City and an associate researcher at the Arizona-Sonora Desert Museum. Dr. Medellín has studied and worked on the ecology and conservation of mammals in Mexico for 25 years. After completing his undergraduate studies at the University of Mexico he obtained his Ph.D. from the University of Florida. Dr. Medellín's work in rainforests, deserts, and montane forests has included diverse approaches: community ecology, plant-animal interactions, population biology, and more recently, molecular ecology. He has produced more than 70 publications, including more than 40 scientific papers in international journals and 6 books and book chapters on bat ecology and conservation, mammal diversity analyses, and conservation of large mammals. Dr. Medellín was head of the Wildlife Department of the Mexican federal government from 1995 to 1996. He has been president of the Mexican Society of Mammalogists and has served as chair of the Committee for International Relations. He currently chairs the Latin American Fellowship Committee of the American Society of Mammalogists, and has been a member of the Board of Directors for that society for 6 years and was elected in June 2004 to a third 3-year term. He is a member of the Scientific Advisory Board of Bat Conservation International, and he is founder and director of the 10-year-old Program for the Conservation of Bats of Mexico.

Taylor Ricketts is the director of World Wildlife Fund conservation science program. His research is on global patterns of biodiversity and threats, ecological and economic consequences of habitat fragmentation, and interactions between people and nature in agricultural landscapes. Dr. Ricketts analyzes compiled data sets for insight about the global picture of biodiversity, how patterns in biodiversity relate to those of human threats, and how the information can be applied to support conservation efforts. Dr. Ricketts's field studies focus on the value of tropical forest fragments as sources of wild pollinators for neighboring coffee crops. That project is part of his long-standing interests in the interactions between habitat fragments and surrounding agricultural areas and in improving the potential of those landscapes to support native biodiversity. Dr. Ricketts received his Ph.D. from Stanford University and has received numerous awards for his work from the Society for Conservation Biology, the National Science Foundation, the Summit Foundation, and others.

Gene E. Robinson joined the faculty of the University of Illinois, Urbana-Champaign, in 1989 and is the university's G. William Arends Professor of Integrative Biology. He is also the director of the University of Illinois Bee Research Facility, director of the Neuroscience Program, theme leader at the Institute for Genomic Biology, and a professor of entomology with affiliate appointments in the Departments of Cell & Developmental Biology and

Animal Biology and in the Beckman Institute of Science and Technology. Dr. Robinson obtained his Ph.D. in entomology from Cornell University in 1986. He is the author or coauthor of more than 150 publications, including articles published in *Nature*, *Science*, and the *Proceedings of the National Academy of Sciences*. He pioneered the application of genomics to the study of social behavior, led the effort to gain approval from the National Institutes of Health for sequencing the honey bee genome, and heads the Honey Bee Genome Sequencing Consortium. Dr. Robinson has been honored as a University Scholar, Fulbright Fellow, and Guggenheim Fellow. He is a member of the American Academy of Arts & Sciences and NAS.

Allison A. Snow is a professor of evolution, ecology, and organismal biology at the Ohio State University in Columbus. Dr. Snow received her Ph.D. in botany from the University of Massachusetts. She is noted for her expertise in the evolutionary ecology of plant populations, including breeding systems, pollination ecology, and conservation biology. Dr. Snow's research focuses on hybridization as a stimulus for rapid evolution in weedy and invasive plants. She has published widely in peer-reviewed journals, and she has produced several technical reports and book chapters on transgenic plants, pollination ecology, and gene flow. Dr. Snow is an Aldo Leopold Leadership Fellow of the Ecological Society of America and is the current president of the Botanical Society of America. She served on the National Research Council's Committee on Genetically Modified Pest-Protected Plants and on the Committee on Biological Confinement of Genetically Engineered Organisms.

Scott M. Swinton is a professor of agricultural economics at Michigan State University in East Lansing. Dr. Swinton teaches agricultural production economics, agribusiness operations management, and ecological economics. He received his M.S. from Cornell University and Ph.D. from the University of Minnesota. His economic research on agricultural production and environmental management focuses on technology evaluation and policy analysis. He concentrates on understanding the conditions required for business profitability to be compatible with environmental stewardship. Dr. Swinton also is engaged in research on agricultural and natural resource management in Latin America and Africa. He has published more than 45 journal articles and edited 3 books. He currently serves on the editorial board of the *American Journal of Agricultural Economics*.

Leonard B. Thien is a professor in the Department of Cell and Molecular Biology at Tulane University in New Orleans, Louisiana. He received an M.S. in botany (systematics and evolution) from Washington University, St. Louis, and a Ph.D. in botany (evolution) from the University of

California, Los Angeles. Dr. Thien's research is on the pollination biology of ancient plants in the ANITA group—the first three branches of the flowering plant phylogenetic tree. Dr. Thien has published papers on the pollination mechanisms and population structure of *Amborella* (sister to the angiosperms). He also elucidated the pollination mechanisms and breeding systems of *Illicium* and *Trimenia* (the third branch of the angiosperm cladogram). In North America, Dr. Thien's work includes mosquito pollination in orchids (*Habenaria* in northern Wisconsin and Canada), bee pollination of orchids in the bogs of northern Wisconsin, and beetle and fly pollination of magnolia in the southern United States and Mexico. In 1991, Dr. Thien was elected a fellow of the American Association for the Advancement of Science for his work on pollination mechanisms in basal (ancient) angiosperms. Dr. Thien is working with a group of Chinese scientists on the pollination of *Schisandra* (ANITA group, third branch) in North America and Southeast Asia. The work involves pollination, construction of a DNA cladogram, and an analysis of all aspects of the breeding system.

F. Christian Thompson is a research entomologist at the Systematic Entomology Laboratory of the U.S. Department of Agriculture and a scientist in the Department of Entomology at the Smithsonian Institution. He received his B.S. and Ph.D. from the University of Massachusetts, Amherst. His research is in the systematics of flower flies (Syrphidae). He also has expertise on other families of agricultural concern (Anthomyiidae, Asilidae, Braulidae, Phoridae, and Pipunculidae) and other groups important for biological control (Pipunculidae, Conopidae). His current research includes projects on the flower flies of Costa Rica, nearctic flower flies, and genera of flower flies.

B

Presentations to the Committee

**Keck Center, The National Academies
Washington, DC
July 6, 2005**

Perspective of sponsoring agencies
Kevin Hackett, U.S. Department of Agriculture, Agricultural Research
Service
William Walker, U.S. Geological Survey

Comments from the North American Pollinator Protection Campaign:
Information sources from NAPP
Laurie Adams, North American Pollinator Protection Campaign

**Workshop on the Status of Pollinators in North America
National Academy of Sciences Building
Washington, DC
October 18–19, 2005**

SESSION 1: Direct and Indirect Indication of Pollinator Population Size

Databases on pollinators in North America
Terry Griswold, U.S. Department of Agriculture, Agricultural Research
Service

Databases on pollinators in North America—natural history collections
John Ascher, American Museum of Natural History

Databases on pollinators in North America
Sam Droege, U.S. Geological Survey, Patuxent Wildlife Research Center

Databases on pollinators in North America and the Monarch Watch
Orley Taylor, University of Kansas

Databases on pollinators in Mexico
Ma. del Coro Arizmendi, National Autonomous University of Mexico

Long-term bee survey
Robert Minckley, Rochester University

Xerces Society's red list
Scott Hoffman Black, Xerces Society

SESSION 2: Possible Causes of Pollinator Decline

Effects of climate change on pollinator populations
Jessica Hellmann, University of Notre Dame

Effects of pollinator declines on the ecological genetics of plant
populations
Kent Holsinger, University of Connecticut

Demographic and genetic factors as causes of pollinator decline
Laurence Packer, York University, Canada

Impact of landscape ecology, habitat fragmentation, and agricultural
intensification on pollinator populations
Nick Haddad, North Carolina State University

Impact of invasive species on pollinator populations and the implications
for land and resource management
Diane Larson, U.S. Geological Survey, North Prairie Wildlife Research
Center

Factors that influence population sizes in bumble bees and other members
of the native bee community
Robbin Thorp, University of California, Davis

Causes and consequences on honey bee decline with emphasis on the
almond industry
Marla Spivak, University of Minnesota, St. Paul

Causes and consequences on honey bee decline
Joe Traynor, Scientific Ag Co.

SESSION 3: Consequences of Pollinator Decline

Consequences of population decline in nectar-feeding bats
Ted Fleming, University of Miami

Effects of pollinator declines on the ecological genetics of plant
populations
Tia-Lynn Ashman, University of Pittsburgh

Environmental Economics of Pollinator Decline
Stephen Polasky, University of Minnesota

Biological and economic factors that impact the overall health of the
honey bee industry
Daniel Weaver, B. Weaver Apiaries and the American Bee Keeping
Federation

Conservation of biodiversity of pollinators in natural and agro ecosystems
Simon G. Potts, University of Reading

**Beckman Center, The National Academies
Irvine, CA
January 14, 2006**

The current status of the alfalfa leafcutting bee as a pollinator of alfalfa
seed
Ron Bitner, International Pollination Systems

Monitoring schemes and citizen science program for pollinators
Gordon W. Frankie, University of California, Berkeley

Pollination decline: Is it the canary in the mine shaft?
Jerry Hayes, Florida Department of Agriculture and Consumer Services

Economics of pollinator services and potential policy implications
Daniel Sumner, University of California, Davis

C

Recently Extinct Insects from Around the World

Scientific Name	Common Name
Coleoptera	
<i>Dryophthorus distinguendus</i>	Weevil [unnamed]
<i>Dryotribus mimeticus</i>	Weevil [unnamed]
<i>Karocolens tuberculatus</i>	Weevil [unnamed]
<i>Macrancyclus linearis*</i>	Weevil [unnamed]
<i>Mecodema punctellum</i>	Ground beetle [unnamed] (New Zealand)
<i>Megadytes ducalis</i>	Water beetle [unnamed] (Brazil)
<i>Oedemasyllus laysanensis</i>	Weevil [unnamed] (Hawaiian Islands)
<i>Pentarthrum blackburni</i>	Blackburn weevil
<i>Rhantus orbigny</i>	Water beetle [unnamed] (New Caledonia)
<i>Rhantus papuanus</i>	Water beetle [unnamed] (New Guinea)
<i>Rhyncogonus bryani</i>	Weevil [unnamed]
<i>Siettitia balsetensis</i>	Perrin cave beetle
<i>Trigonoscuta rossi</i>	Fort Ross weevil
Diptera	
<i>Campsicnemus mirabilis</i>	Longlegged fly [unnamed] (Hawaii)
<i>Drosophila lanaiensis</i>	Vinegar fly [unnamed] (Hawaii)
<i>Stonemyia volutina</i>	Volutine stoneyian tabanid fly
Ephemeroptera	
<i>Acanthometropus pecatonica</i>	Pecatonica River mayfly
<i>Pentagenia robusta</i> Robust	Burrowing mayfly [unnamed]
Homoptera	
<i>Claviccoccus erinaceus</i>	Mealy bug [unnamed]
<i>Phyllococcus oahuensis</i>	Aphid [unnamed] Hawaii
Lepidoptera	
<i>Agrotis crinigera*</i>	Noctuid moth [unnamed]*
<i>Agrotis fasciata*</i>	Midway noctuid moth*
<i>Agrotis kerri*</i>	Kerr's noctuid moth*

Scientific Name	Common Name
<i>Agrotis photophila</i> *	Noctuid moth [unnamed]*
<i>Agrotis procellaris</i> *	Procellaris grotis noctuid moth*
<i>Argyresthia castaneela</i> *	Chestnut ermine moth*
<i>Coleophora leucochrysellata</i> *	Casebearer moth [unnamed]
<i>Deloneura immaculate</i> *	Hairsteak butterfly [unnamed]*
<i>Ectodemia castaneae</i> *	American chestnut moth*
<i>Genophantis leabi</i> *	Looper moth [unnamed]*
<i>Glaucopsyche xerces</i> *	Xerces blue*
<i>Lepidochrysops hypopolia</i> *	Hairsteak butterfly [unnamed] (South Africa)
<i>Levuana iridescens</i> *	Levuana moth*
<i>Libythea cinyras</i> *	Snout butterfly [unnamed] (Mauritius)*
<i>Maculinea alcon arenaria</i> *	Dutch alcon blue*
<i>Oeobia</i> sp.*	Pyralid moth [unnamed]*
<i>Parnassius clodius strohbeeni</i> *	Strohbeen parnassian*
<i>Scotorythra megalophylla</i> *	Kona giant looper moth*
<i>Scotorythra nesiotis</i> *	Ko'olau giant looper moth*
<i>Scotorythra paratactis</i> *	Hawaiian hopseed looper moth*
<i>Speyeria adiastra atossa</i> *	Atossa fritillary*
<i>Tischeria perplexa</i> *	Chestnut clearwing moth*
Odonata	
<i>Megalagrion jugorum</i>	Jugorum megalagrion damselfly
Orthoptera	
<i>Sympetrum dilatatum</i>	Dragonfly [unnamed]
Orthoptera	
<i>Conozoa hyalina</i>	Central Valley grasshopper
<i>Neduba extincta</i>	Antioch Dunes shieldback katydid
Plecoptera	
<i>Alloperla roberti</i>	Robert's stonefly
Trichoptera	
<i>Rhyacophila amabilis</i>	Castle Lake caddisfly
<i>Triaenodes phalacris</i>	Athens caddisfly
<i>Triaenodes tridonata</i>	Three-tooth caddisfly

*Potential pollinator; species is known to visit flowers for nectar or pollen.

SOURCE: Adapted from <http://extinctanimals.petermaas.nl/>.

D

Endangered Insects in the Continental United States

Scientific Name	Common Name
Coleoptera	
<i>Batrisodes texanus</i>	Coffin cave mold beetle
<i>Batrisodes ventyivi</i>	Helotes mold beetle
<i>Brychius hungerfordi</i>	Hungerford crawling water beetle
<i>Cicindela ohlone</i>	Ohlone tiger beetle
<i>Heterelmis comalensis</i>	Comal Springs riffle beetle
<i>Nicrophorus americanus</i>	American burying beetle
<i>Polyphylla barbata</i>	Mount Hermon June beetle
<i>Rhadine exilis</i>	Ground beetle [unnamed]
<i>Rhadine infernalis</i>	Ground beetle [unnamed]
<i>Rhadine persephone</i>	Tooth Cave ground beetle
<i>Stygoparnus comalensis</i>	Comal Springs dryopid beetle
<i>Texamaurops reddelli</i>	Kretschmarr Cave mold beetle
Diptera	
<i>Rhaphiomidas terminatus abdominalis</i> *	Delhi Sands flower-loving fly*
Lepidoptera	
<i>Apodemia mormo langei</i>	Lange metalmark butterfly*
<i>Boloria acrocneuma</i> *	Uncompahgre fritillary butterfly*
<i>Callophrys mossii bayensis</i> *	San Bruno elfin butterfly*
<i>Euphilotes battoides allyni</i> *	El Segundo blue butterfly*
<i>Euphilotes enoptes smithi</i> *	Smith blue butterfly*
<i>Euphydryas editha quino</i> (=E. e. <i>wrighti</i>)*	Wright's euphydryas (Quino checkerspot butterfly)*
<i>Glaucopsyche lygdamus palosverdesensis</i> *	Palos Verdes blue butterfly*
<i>Heracles aristodemus ponceanus</i> *	Schaus swallowtail butterfly*
<i>Icaricia icarioides fenderi</i> *	Fender blue butterfly*
<i>Icaricia icarioides missionensis</i> *	Mission blue butterfly*
<i>Lycaeides argyrognomon lotis</i> *	Lotis blue butterfly*

Scientific Name	Common Name
<i>Lycaeides melissa samuelis</i> *	Karner blue butterfly*
<i>Manduca blackburni</i> *	Blackburn sphinx moth*
<i>Neonympha mitchellii francisci</i> *	Saint Francis satyr butterfly*
<i>Neonympha mitchellii mitchellii</i> *	Mitchell satyr butterfly*
<i>Pseudocopaeodes eunus obscurus</i> *	Carson wandering skipper*
<i>Pyrgus ruralis lagunae</i> *	Laguna Mountains skipper*
<i>Speyeria callippe callippe</i> *	Callippe silverspot butterfly*
<i>Speyeria zerene behrensii</i> *	Behren silverspot butterfly*
<i>Speyeria zerene myrtleae</i> *	Myrtle silverspot butterfly*
Odonata	
<i>Somatochlora hineana</i>	Hine emerald dragonfly
Orthoptera	
<i>Trimerotropis infantilis</i>	Zayante band-winged grasshopper

*Potential pollinator; species is known to visit flowers for nectar or pollen.

SOURCE: Adapted from http://ecos.fws.gov/tess_public/SpeciesReport.do?kingdom=I&listingType=L.

E

Bee Species in Decline in North America

Bombus (Bombus) franklini (Frison)
Bombus (Bombus) occidentalis Greene
Bombus (Bombus) affinis Cresson
Bombus (Bombus) terricola Kirby
Bombus (Fervidobombus) sonorus Say
Bombus (Fervidobombus) pensylvanicus (DeGeer)
Epeoloides pilosula (Cresson)

SOURCE: Robbin Thorp, University of California, Davis.

F

Meetings and Conferences on Pollinator Issues 1979–2006

Event	Sponsor	Location	Date	Publication
Pesticide–Pollinator Interactions	National Research Council Canada	Toronto, Ont.	1979–1980	NRCC, 1981
Alternative Pollinators for Ontario’s Crops		Guelph, Ont.	April 12, 1986	<i>Proceedings of the Entomological Society of Ontario</i> , 118 (1988)
National Workshop on Bee and Pollination Research	Agriculture Canada	Winnipeg, Man.	April 4–5, 1989	Agriculture Canada
International Workshop on Non- <i>Apis</i> Bees	U.S. Department of Agriculture	Logan, Utah	Aug. 10–13, 1992	
Tri-National Forgotten Pollinators Campaign	Arizona–Tucson Desert Museum	Phoenix, Ariz.	1995–1999	Various, including Buchmann and Nabhan, 1996
Conservation of Bees	International Bee Research Association; Linnaean Society	United Kingdom	April 1995	Matheson et al., 1996
Bees and Crop Pollination—Crisis, Crossroads, Conservation	Entomological Society of America	Burlington, Vt.	Feb. 26, 1997	Stubbs and Drummond, 2001

Event	Sponsor	Location	Date	Publication
Pollinators and Mother Earth: Global Perspectives in Productivity, Diversity, and Behavior	Entomological Society of Canada	Edmonton, Alta.	Oct. 4–8, 1997	None
For Non-Native Crops, Whence Pollinators of the Future?	Entomological Society of America	Las Vegas, Nev.	Nov. 8–12, 1998	Strickler and Cane, 2003
Saving America's Pollinators	National Fish and Wildlife Foundation, Coevolution Institute, National Zoological Park	Washington, D.C.	June 18, 1998	None
Pollinating Bees: The Conservation Link Between Agriculture and Nature	Brazilian Ministry of Environment	São Paulo, Brazil	Oct. 7–9, 1998	Kevan et al., 2002
Workshop on Declining Pollinators	U.S. Department of Agriculture, U.S. Department of Interior	Logan, Utah	May 27–28, 1999	USGS/BRD/ITR-2000-0007
Causes and Extent of Declines Among Native Invertebrate Pollinators: Detection, Evidence and Consequences	National Center for Ecological Analysis and Synthesis	Santa Barbara, Calif.	October 1999	<i>Conservation Ecology</i> 5 (2001)
North American Pollinator Protection Campaign	Coevolution Institute	Washington, D.C., and area	Annually since 2000	None, but see http://www.nappc.org
International Congress of Entomology		Foz Iguazu, Brazil	2000	None
National Conference on Pollination Ecology and Its Contribution to Conservation and Biodiversity		Andhra University, India	Feb. 22–24, 2000	Souvenir and abstracts published by Andhra University, Visakhapatnam, Andhra Pradesh, India
FAO International Pollinators Initiative, Plan of Action	United Nations Food and Agriculture Organization	Rome, Italy	Nov. 14–16, 2000	See http://www.fao.org/

Event	Sponsor	Location	Date	Publication
Protecting and Promoting Our Pollinators	Entomological Society of Quebec, Entomological Society of Canada, Entomological Society of America	Montreal, Que.	Dec. 3–6, 2000	None
Managing Biodiversity in Agricultural Ecosystems: Convention on Biological Diversity		Montreal, Que.	Nov. 8–10, 2001	See http://www.unu.edu/env/plec/cbd
First Meeting of the African Pollinators Initiative		Nairobi, Kenya	Feb. 18–22, 2002	Web site
Pollinators Workshop		Mabula, South Africa	June 27–29, 2003	Eardley et al., 2006
São Paulo Declaration on Pollinators + 5 Forum		São Paulo, Brazil	Oct. 27–30, 1998	Kevan and Imperatriz-Fonseca, 2002
International Workshop on Solitary Bees and their Role in Pollination		Beberibe, Ceará, Brazil	April 26–29, 2004	Freitas and Pereira, 2004
United Nations Convention on Biodiversity, Conference of the Parties, General Meeting 8		Curitiba, Brazil	March 2006	<i>Pollinators and Pollination: A Resource Book for Policy and Practice</i>

G

Methods for Analyzing Status of Pollinators

DIRECT MONITORING

The status of pollinator populations and assemblages can be assessed in many ways, both direct and indirect. Because a decline is a decrease in abundance over time, long-term surveys are the most valuable indicators for assessing pollinator status. The inherent year-to-year variability of pollinator populations, however, makes trend analysis difficult. Roubik (2001) surveyed various studies of the population dynamics of 59 bee species—short-term projects (2–4 years) and longer studies (17–21 years, all tropical)—and reported that the species' mean abundances had varied by factors of 2.06 for temperate bees and 2.16 for tropical bees (see Appendix F). Because the natural variability of populations can lead them to halve or double the average in 1-year intervals, reliable population trends cannot be determined from short-term studies, and even trends from long-term studies might not be definitive.

Although direct monitoring of natural populations is invaluable for identification of pollinator population trends, the ease of use and the accuracy of monitoring techniques differ among species. Some of the best examples of large-scale, long-term monitoring involve birds. Banding records from research stations and the annual Audubon Christmas Bird Counts have combined to provide more than a century's worth of census data on the birds of North America (<http://www.audubon.org/bird/cbc/>). Focused research on a handful of species of particular interest—such as monarch butterflies or specific threatened or model species, for example—also can provide an accurate picture of population trends (for example, Ehrlich and Hanski, 2004).

Visual counts can be used effectively for direct assessment of abundance for vertebrate pollinators, such as bats and hummingbirds. Mist nets can also be used to capture these flying vertebrates, and their density can be accurately estimated because the individuals are large enough to be banded or marked by some other method. Direct assessment of insect pollinator abundance is typically conducted by observation at the flowers they visit. Pollinating insects are much more conspicuous when visiting flowers than they are in transit among foraging areas or when engaged in other activities; for example, ground-nesting bees' nests can be difficult to find. One method is to count all visitors to a set number of flowers, generally of a single species, during a specified period (typically 10 minutes), when meteorological observations are simultaneously recorded (Kearns and Inouye, 1993). In addition to providing an estimate of pollinator visitation rate, this method allows a snapshot assessment of the dependence of insect activity on environmental factors, such as temperature, humidity, wind, and light (for example, McCall and Primack, 1992). However, one problem with assessing pollinator populations based on flower visits is that floral abundance and diversity often vary greatly as well.

An alternative method for estimating insect pollinator abundance involves counting or collecting individuals along a transect (for example, 1 m × 2.5 m, or 1 m for a fixed period), as in a Pollard walk census for butterflies (Caldas and Robbins, 2003), or in a recent survey of bumble bee populations (Knop et al., 2006). Bees that are not collected can be captured, marked, and released to distinguish individuals and prevent redundant counting (Hines and Hendrix, 2005). Netting at flowers along transects in permanent, one-hectare plots also has been used for native bees (Cane et al., 2000). Insects that readily adopt artificial nest sites—such as nest boxes for bumble bees or trap nests for solitary bees—can be monitored by placing the nests in appropriate habitats. A disadvantage of this method is that adoption rates can be low (as is often the case for bumble bees; Inouye, unpublished). Pollinators that can be manipulated by reward—euglossine bees are attracted to terpene-soaked blotter paper (Dodson et al., 1969; Roubik, 1989; Roubik and Hanson, 2004), hummingbirds will consume artificial nectar from feeders, moths fly to traps baited with fermenting fruit—are more easily monitored than are those that cannot be reliably attracted to a particular location.

Passive traps that collect insects indiscriminately are not always suitable. Entomologists have long used Malaise traps (screen tents that catch insects and funnel them up into a collecting head) because they work well for many kinds of flies. However, the traps rarely capture butterflies, moths, or bumble bees. The selectivity of pan traps for bees depends on the use of appropriate combinations of trap size, color, and number (S. Droege, Patuxent Wildlife Research Center, presentation to the committee, October 18, 2005),

and pan traps can be used to provide reliable population estimates (Russell et al., 2005). Light traps, which attract insects with mercury vapor lamps (visible and ultraviolet light) or various short- and long-wave ultraviolet lights, are also used to sample insect pollinators (some nocturnal bees, beetles, flies, wasps, moths) in diverse temperate and tropical habitats.

DATABASES

Because direct long-term monitoring studies are so rare, population patterns over time must be ascertained in other ways. Biological databases—taxonomic and genomic databases and information collected from conservation-related enterprises—can often be mined for data on historic patterns of pollinator distribution and, in some cases, abundance.

Specimen databases contain the information associated with vouchers in museum collections. At a minimum, the records show when, where, how, and by whom particular specimens were collected as well as their presumptive identifications. Specimen databases also can hold information about field observations. Museums capture information associated with the specimens in their collections, usually processing information on the best known and most widely studied groups first and then moving on to groups that are less well characterized. It is so widely assumed that mammal and bird species have been described that discovery of an undescribed primate genus (*Rungwecebus*) makes worldwide headlines (Davenport et al., 2006). In contrast, some groups with greater relevance to pollination, such as flies, are so diverse that experts cannot even venture a guess as to what proportion of genera remain to be described.

Specimen databases may be accessible online, and software applications grant access to all available databases together. The Global Biodiversity Information Facility (GBIF) provides a single interface that queries all online specimen databases that conform to community standards and protocols. The GBIF portal provides access to 90 million records from more than 700 collections (<http://www.europe.gbif.net/portal/index.jsp>). Sample queries for the honey bee returned 6,362 records from 9 data providers; most records were from Costa Rica (INBio, 5,920 records). The ruby-throated hummingbird, in contrast, returned 15,912 records from 9 data providers. Although specimen databases are optimal sources for trend information, few museum collections have digital databases of their specimen holdings, particularly of insects.

Character databases document the characteristics that taxonomists use to distinguish groups of organisms, primarily for specialists. The information also can be used to construct interactive identification aids for parataxonomists and citizen-scientists. There are three principal character databases: MorphBank (<http://www.morphbank.net/>) and MorphoBank ([Copyright © National Academy of Sciences. All rights reserved.](http://www.</p></div><div data-bbox=)

morphobank.org/) contain morphological characters, and GenBank (<http://www.ncbi.nlm.nih.gov/Genbank/>) has DNA sequence characters.

Nomenclatural databases provide information and documentation on the scientific names of organisms. They provide the correct (valid) names for species so users have the appropriate search terms for queries in other databases. Like specimen databases, the number of nomenclature databases for particular groups and areas is increasing, and so is the number of software applications that consolidate or provide access to them. The Catalogue of Life, through its annual checklist, provides minimal information on more than a half-million species; all of that information is integrated with the services of GBIF as part of the Electronic Catalogue of Life Names of Known Organisms. The Universal Biological Indexer and Organizer contains approximately 5 million names; the Taxonomic Search Engine searches all major nomenclators; and the Integrated Taxonomic Information System provides the official taxonomy of living organisms for the United States, Canada, and Mexico. Some specialized databases that include pollinator data are the BioSystematic Database of World Diptera and the Hymenoptera Name Server.

Species databases provide information and documentation on organisms. Unfortunately, a comprehensive database does not yet exist, although ultimately, species databases will be transformed into the envisioned Electronic Encyclopedia of Life (Wilson, 2003). Species databases sort information by attributes, such as the pollinators of a given plant, and they provide summaries about species or links to species web pages.

Literature databases compile published information and they comprise the same sources used generally for the biological sciences. Literature databases range from general commercial compilations, such as Biological Abstracts and the Zoological Record, to specialized research databases, such as AnimalBase, which links digital versions of the early zoological literature to personally maintained, but publicly accessible databases. One example is the Pollination Biology Database, maintained by David Inouye at the University of Maryland.

Conservation-oriented databases exist to track and monitor putatively threatened populations of animals and plants. Among them are the NatureServe Explorer and the Heritage Program network; the federal database of species protected by the U.S. Endangered Species Act; and international lists, such as those from the Convention on International Trade in Endangered Species of Wild Fauna and Flora (www.cites.org/) and the World Conservation Union (IUCN; www.redlist.org/). The Heritage Program and NatureServe tracking systems provide a first step in understanding patterns of decline.

Numerous sources of data—including museum collections, naturalists' observations, and accounts published in peer-reviewed literature—contrib-

ute to formal rankings of rarity and abundance making them dynamic and subject to continuing input. In the United States, the Heritage Program has established a global rank system that denotes global, regional, and state-specific rarity. The rank of G1, for example, denotes fewer than five occurrences of a given species or community globally; G2 and G3 represents 6–20 occurrences and 21–100 occurrences, respectively; G4 and G5 denotes apparently abundant globally and demonstrably widely abundant species globally, respectively. The state rankings within the United States are equivalent: S1–S5 parallels G1–G5. Those data are available to the public through NatureServe.org.

H

Xerces Society Red List of Pollinating Insects of North America

A species is placed on the Xerces Society Red List based on consultation with scientists or upon identification by a federal or state agency as endangered, threatened, or at risk.

TABLE H-1 Lepidoptera, Red List Status and North American Distribution

Scientific Name	Common Name	Status	Canada	Mexico	United States
<i>Agathymus evansi</i>	Huachuca giant skipper	Imperiled		SO, CH, CI	AZ
<i>Agathymus mariae</i> (complex inc. <i>gilberti</i>)	Mary giant skipper	Data deficient		CH, CI	NM, TX
<i>Amblyscirtes linda</i>	Linda roadside skipper	Vulnerable			AR, IL, KS, MO, OK, TN
<i>Apodemia mormo langei</i> *	Lange metalmark	Critically imperiled			CA
<i>Atrytone arogos</i>	Arogos skipper	Vulnerable			AL, AR, CO, FL, GA, IA, IL, KS, MN, MO, MS, MT, NC, ND, NE, NJ, NY, OK, PA, SC, TX, WY
<i>Boloria acrocnemata</i> *	Uncompahgre fritillary	Critically imperiled			CO

TABLE H-1 Continued

Scientific Name	Common Name	Status	Canada	Mexico	United States
<i>Boloria alberta</i>	Alberta fritillary	Vulnerable	AB, BC		MT
<i>Calephelis borealis</i>	Northern metalmark	Vulnerable			AR, CT, IL, IN, KY, MD, MO, NJ, NY, OH, OK, PA, VA, WV
<i>Callophrys comstocki</i>	Desert green hairstreak	Imperiled			AZ, CA, CO, NV, UT
<i>Callophrys irus</i> †	Frosted elfin	Imperiled	ON		AL, AR, CT, DC, DE, GA, IL, IN, KS, KY, LA, MA, MD, ME, MI, NC, NH, NJ, NY, OH, OK, PA, RI, SC, TN, TX, VA, WI, WV
<i>Callophrys lanoraieensis</i>	Bog elfin	Vulnerable	NB, NS, ON, QC		ME, NH, NY
<i>Callophrys mossii bayensis</i> *	San Bruno elfin	Critically imperiled			CA
<i>Celotes limpia</i>	Scarce streaky-skipper	Vulnerable		CI	TX
<i>Cyclargus thomasi bethunebakeri</i>	Miami blue	Critically imperiled			FL
<i>Erora laeta</i>	Early hairstreak	Vulnerable	NB, NS, ON, QC		GA, KY, MA, MD, ME, MI, NC, NJ, NY, PA, TN, VA, VT, WI, WV
<i>Erynnis persius persius</i>	Persius duskywing	Imperiled	ON		CT, IN, MA, MD, ME, MI, MN, MO, NH, NJ, NY, PA, RI, VA, VT, WI, WA
<i>Euchloe ausonides insulana</i> †	Island marble	Critically imperiled			CA
<i>Euphilotes battoides allyni</i> *	El Segundo blue	Critically imperiled			CA
<i>Euphilotes baueri</i>	Bauer dotted blue	Imperiled			AZ, CA, NV
<i>Euphilotes enoptes smithi</i> *	Smith blue	Critically imperiled			CA
<i>Euphilotes mojave</i>	Mojave dotted blue	Imperiled		BN	AZ, CA, NV, UT
<i>Euphydryas anicia cloudcrofti</i>	Sacramento Mountains checkerspot	Critically imperiled			NM

continues

TABLE H-1 Continued

Scientific Name	Common Name	Status	Canada	Mexico	United States
<i>Euphydryas editha bayensis</i> *	Bay checkerspot	Critically imperiled			CA
<i>Euphydryas editha quino</i> *	Quino checkerspot	Critically imperiled		BN	CA
<i>Euphydryas editha taylori</i> †	Taylor checkerspot	Critically imperiled	BC		OR, WA
<i>Euphydryas gillettii</i>	Gillett checkerspot	Vulnerable	AB, BC		ID, MT, UT, WY
<i>Euphyes bayensis</i>	Bay skipper	Vulnerable			MS, TX
<i>Euphyes dukesi</i>	Dukes skipper	Vulnerable	ON		AL, AR, FL, GA, IL, IN, KY, LA, MI, MO, MS, NC, OH, SC, TX, VA
<i>Euproserpinus euterpe</i>	Kern primrose sphinx moth	Critically imperiled			CA
<i>Fixsenia [Satyrium] polingi</i>	Poling hairstreak	Imperiled		CI	NM, TX
<i>Glaucopsyche lygdamus palosverdesensis</i> *	Palos Verde blue	Critically imperiled			CA
<i>Heraclides aristodemus ponceanus</i> *	Schaus swallowtail	Critically imperiled			FL
<i>Hesperia dacotae</i> †	Dakota skipper	Imperiled	MB, SK		IA, IL, MN, ND, SD
<i>Hesperia leonardus montana</i> *	Pawnee montane skipper	Imperiled			CO
<i>Hesperia ottoe</i> †	Ottoe skipper	Vulnerable	MB		CO, IA, IL, IN, KS, MI, MN, MO, MT, ND, NE, OK, SD, TX, WI, WY
<i>Hesperopsis graciellae</i>	Macneil's saltbush sootywing	Vulnerable		BN, BS	AZ, CA, NV, UT
<i>Icaricia icarioides fenderi</i> *	Fender blue	Critically imperiled			OR
<i>Icaricia icarioides missionensis</i> *	Mission blue	Critically imperiled			CA
<i>Lycaeides idas lotis</i> *	Lotis blue	Critically imperiled (possibly extinct)			CA

continues

TABLE H-1 Continued

Scientific Name	Common Name	Status	Canada	Mexico	United States
<i>Lycaeides melissa samuelis</i> *†	Karner blue	Critically imperiled	ON		IL, IN, MI, MN, NH, NY, OH, WI
<i>Manduca blackburni</i> *	Blackburn sphinx moth	Critically imperiled			HI
<i>Mitoura hesseli</i>	Hessel hairstreak	Vulnerable			AL, CT, DE, FL, GA, MA, MD, ME, NC, NH, NJ, NY, RI, SC, VA
<i>Neonympha mitchellii francisci</i> *	St. Francis satyr	Critically imperiled			NC
<i>Neonympha mitchellii mitchellii</i> *	Mitchell satyr	Critically imperiled			IN, MI, OH
<i>Oarisma powesheik</i> †	Powesheik skipperling	Imperiled	MB		IA, IL, MI, MN, ND, SD, WI
<i>Papilio joanae</i>	Ozark woodland swallowtail	Vulnerable			AR, MO (KY?)
<i>Polites mardon</i>	Mardon skipper	Imperiled			CA, OR, WA
<i>Problema bulenta</i>	Rare skipper	Imperiled			DE, GA, MD, NC, NJ, SC, VA
<i>Problema byssus</i>	Byssus skipper	Vulnerable			AL, AR, FL, GA, IA, IL, IN, KS, MO, MS, NC, OK, SC, TX, WI
<i>Pseudocopaodes eunus obscurus</i> *	Carson wandering skipper	Critically imperiled			CA, NV
<i>Pyrgus ruralis lagunae</i> *	Laguna Mountains skipper	Critically imperiled			CA
<i>Satyrrium kingi</i>	King hairstreak				AL, AR, DE, FL, GA, MD, MS, NC, TX, VA
<i>Speyeria callippe callippe</i> *	Callippe silverspot	Critically imperiled			CA
<i>Speyeria diana</i>	Diana fritillary	Vulnerable			AL, AR, GA, IN, KY, MO, NC, OH, OK, SC, TN, VA, WV

continues

TABLE H-1 Continued

Scientific Name	Common Name	Status	Canada	Mexico	United States
<i>Speyeria idalia</i>	Regal fritillary	Vulnerable	MB, ON		AR, CO, CT, DC, DE, IA, IL, IN, KS, KY, MA, MD, ME, MI, MN, MO, NC, ND, NE, NH, NJ, NY, OH, OK, PA, RI, SD, VA, VT, WI, WV, WY
<i>Speyeria zerene behrensii</i> *	Behren silverspot	Critically imperiled			CA
<i>Speyeria zerene hippolyta</i> *	Oregon silverspot	Critically imperiled			CA, OR, WA
<i>Speyeria zerene myrtleae</i> *	Myrtle silverspot	Critically imperiled			CA
<i>Stallingsia maculosus</i>	Manfreda giant-skipper	Imperiled		NL, ?	TX

KEY: *Imperiled*, at high risk of extinction because of highly restricted range, rare populations (often 20 or fewer), steep declines, or other factors; *data deficient*, inadequate information for assessment of risk category because of a lack of information about population size or about threats to the population or because of taxonomic uncertainty about the validity of the taxon; *vulnerable*, at moderate risk of extinction because of restricted range, relatively rare populations (often 80 or fewer), recent and widespread declines, or other factors; *critically imperiled*, at high risk of extinction because of extreme rarity of populations (often 5 or fewer), steep declines, or other factors; *possibly extinct*, missing or known only from historical occurrences but with some hope of rediscovery.

*Listed under the terms of the U.S. Endangered Species Act.

†Listed under the terms of Canada's Species at Risk Act.

SOURCE: Adapted from Shepherd, M.D., D.M. Vaughan, and S.H. Black (Eds). *Red List of Pollinator Insects of North America*. CD-ROM Version 1 (May 2005). Xerces Society for Invertebrate Conservation, Portland, Oregon, http://www.xerces.org/Pollinator_Red_List/Table_Lepidoptera.htm.

TABLE H-2 Hymenoptera, Red List Status and North American Distribution

Scientific Name	Common Name	Status	Canada	Mexico	United States
<i>Andrena aculeata</i>		Vulnerable			Columbia River Basin
<i>Andrena winnemuccana</i>		Vulnerable (data deficient)			OR
<i>Ashmeadiella sculleni</i>		Vulnerable			OR, NV
<i>Bombus affinis</i> (subgenus <i>Bombus</i>)		Vulnerable			
<i>Bombus franklini</i> (see also subgenus <i>Bombus</i>)	Franklin bumble bee	Critically imperiled (possibly extinct)			CA, OR
<i>Bombus lucorum</i> (subgenus <i>Bombus</i>)		Vulnerable			
<i>Bombus occidentalis</i> (subgenus <i>Bombus</i>)		Vulnerable			
<i>Bombus terricola</i> (subgenus <i>Bombus</i>)		Vulnerable			
<i>Calliopsis barri</i>		Vulnerable	MB, ON, SK		ID, OR
<i>Epeoloides pilosula</i>		Critically imperiled			CT, GA, MA, MD, MI, MT, NC, ND, NJ, OH, PA, NY, VA, WI, WV, WA
<i>Eucera douglasiana</i>		Vulnerable (data deficient)			
<i>Eucera frater lata</i>		Vulnerable (data deficient)			Columbia River Basin
<i>Halictus harmonius</i>		Critically imperiled			CA
<i>Halictus pinguimentus</i>		Data deficient		BN	
<i>Hesperapis kayella</i>		Vulnerable (data deficient)			ID, NV
<i>Hoplitis orthognathus</i>		Vulnerable			ID, OR, NV
<i>Hoplitis producta subgracilis</i>		Vulnerable			Columbia River Basin
<i>Hylaeus akoko</i>		Critically imperiled			HI

continues

TABLE H-2 Continued

Scientific Name	Common Name	Status	Canada	Mexico	United States
<i>Hylaeus anomalus</i>	Anomalous yellow-faced bee	Critically imperiled (possibly extinct)			HI
<i>Hylaeus anthracinus</i>		Critically imperiled			HI
<i>Hylaeus assimulans</i>		Critically imperiled			HI
<i>Hylaeus dimidiatus</i>		Critically imperiled			HI
<i>Hylaeus facilis</i>	Easy yellow-faced bee	Critically imperiled			HI
<i>Hylaeus finitimus</i>		Critically imperiled (possibly extinct)			HI
<i>Hylaeus flavifrons</i>		Critically imperiled			HI
<i>Hylaeus gliddena</i>		Critically imperiled (possibly extinct)			HI
<i>Hylaeus hiliaris</i>		Critically imperiled			HI
<i>Hylaeus hula</i>		Imperiled			HI
<i>Hylaeus kona</i>		Critically imperiled			HI
<i>Hylaeus kuakea</i>		Critically imperiled			HI
<i>Hylaeus longiceps</i>		Critically imperiled			HI
<i>Hylaeus lunicraterius</i>		Vulnerable			ID
<i>Hylaeus mana</i>		Critically imperiled			HI
<i>Hylaeus mauiensis</i>		Critically imperiled (possibly extinct)			HI
<i>Hylaeus melanothrix</i>		Critically imperiled			HI
<i>Hylaeus nalo</i>		Critically imperiled (possibly extinct)			HI

continues

TABLE H-2 Continued

Scientific Name	Common Name	Status	Canada	Mexico	United States
<i>Hylaeus niloticus</i>		Critically imperiled (possibly extinct)			HI
<i>Hylaeus ombrias</i>		Critically imperiled			HI
<i>Hylaeus paradoxicus</i>		Critically imperiled			HI
<i>Hylaeus perspicuus</i>		Critically imperiled (possibly extinct)			HI
<i>Hylaeus psammobius</i>		Critically imperiled			HI
<i>Hylaeus satelles</i>		Critically imperiled			HI
<i>Hylaeus simplex</i>	Simple yellow-faced bee	Critically imperiled			HI
<i>Hylaeus solaris</i>		Critically imperiled			HI
<i>Macropis steironema opaca</i>		Critically imperiled (possibly extinct)			WA
<i>Osmia ashmeadii</i>		Critically imperiled			OR
<i>Osmia cascadica</i>		Vulnerable			OR, WA
<i>Perdita accepta</i>		Data deficient			OR
<i>Perdita barri</i>		Data deficient			ID
<i>Perdita crassibirta</i>		Data deficient			WA
<i>Perdita salicis euxantha</i>		Vulnerable			ID, OR
<i>Perdita salicis sublaeta</i>		Vulnerable			OR
<i>Perdita similis pascoensis</i>		Vulnerable			WA
<i>Perdita wyomingensis sculleni</i>		Vulnerable			Columbia River Basin
<i>Perdita wyomingensis wyomingensis</i>		Data deficient			WY

continues

Scientific Name	Common Name	Status	Canada	Mexico	United States
<i>Protandrena subdilatifipes</i>		Vulnerable			WY
<i>Protodufourea wasbaueri</i>		Data deficient			AZ, CA
<i>Sphecodogastra antiochensis</i>		Critically imperiled			

KEY: *Vulnerable*, at moderate risk of extinction because of restricted range, relatively rare populations (often 80 or fewer), recent and widespread declines, or other factors; *data deficient*, inadequate information for assessment of risk category because of a lack of information about population size or about threats to the population or because of taxonomic uncertainty about the validity of the taxon; *critically imperiled*, at high risk of extinction because of extreme rarity of populations (often 5 or fewer), steep declines, or other factors; *possibly extinct*, missing or known only from historical occurrences but with some hope of rediscovery; *imperiled*, at high risk of extinction because of highly restricted range, rare populations (often 20 or fewer), steep declines, or other factors.

SOURCE: Adapted from Shepherd, M.D., D.M. Vaughan, and S.H. Black (Eds). *Red List of Pollinator Insects of North America*. CD-ROM Version 1 (May 2005). Xerces Society for Invertebrate Conservation, Portland, Oregon, http://www.xerces.org/Pollinator_Red_List/Table_Bees.htm.

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Annual Bee Variability of Bee Abundances

Family	Genus	Species	Annual Variability	Years	Reference
Apidae	<i>Apis</i>	1	5.04	10	Roubik and Wolda, 2001
Apidae	<i>Centris</i>	1	1.77	4	Roubik, 1989; unpublished data
Apidae	<i>Centris</i>	1	4.74	17	Roubik and Wolda, 2001
Apidae	<i>Euglossini</i>	6	1.77	2	Pearson and Dressler, 1985
Apidae	<i>Euglossini</i>	32	1.36	20	Roubik, 2001
Apidae	<i>Meliponini</i>	10	4.06	17	Roubik and Wolda, 2001
Colletidae	<i>Ptiloglossa</i>	1	2.45	17	Roubik and Wolda, 2001
Halictidae	<i>Megalopta</i>	2	2.15	17	Roubik and Wolda, 2001
Halictidae	<i>Rhinetula</i>	1	3.45	17	Roubik and Wolda, 2001
Megachilidae	<i>Megachile</i>	3	2.07	3	Frankie et al., 1998
Megachilidae	<i>Osmia</i>	1	2.46	2-3	Frankie et al., 1998

NOTE: Annual variability in bee abundance was determined from short- and long-term censuses in two tropical regions (Peru and Panama) and one temperate region (California).

SOURCE: Adapted from Roubik, 2001.

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PLATE 1 Structure of a flower (*Frasera speciosa*, Gentianaceae; visited by the bumble bee *Bombus flavifrons*). Photo by David Inouye, University of Maryland, College Park.



PLATE 2 Pollinating insects, clockwise from top left: honey bee (*Apis mellifera*, photo by S. Buchmann, University of Arizona, Tucson); sphinx moth (*Hyles lineata*, photo by W. May); yucca moths (*Tegeticula yuccasella*, photo by W. May); a fly (Bombyliidae, photo by D. Inouye, University of Maryland, College Park).



PLATE 3 Lesser long-nosed bat (*Leptonycteris nivalis*), a mammalian pollinator (photo © Merlin D. Tuttle, Bat Conservation International, reprinted with permission).



PLATE 4 Hummingbird, an avian pollinator (photo by W. May).