



Endangered Mutualisms: The Conservation of Plant-Pollinator Interactions

Author(s): Carol A. Kearns, David W. Inouye and Nickolas M. Waser

Source: *Annual Review of Ecology and Systematics*, Vol. 29 (1998), pp. 83-112

Published by: Annual Reviews

Stable URL: <http://www.jstor.org/stable/221703>

Accessed: 14-11-2016 15:23 UTC

REFERENCES

Linked references are available on JSTOR for this article:

http://www.jstor.org/stable/221703?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at

<http://about.jstor.org/terms>



Annual Reviews is collaborating with JSTOR to digitize, preserve and extend access to *Annual Review of Ecology and Systematics*

ENDANGERED MUTUALISMS: The Conservation of Plant-Pollinator Interactions

Carol A. Kearns^{1,4} *David W. Inouye*^{2,4} and
Nickolas M. Waser^{3,4}

¹EPO Biology, Environmental Residential Academic Program, C.B.176, University of Colorado, Boulder, Colorado 80309; ²Department of Biology, University of Maryland, College Park, Maryland 20742; ³Department of Biology, University of California, Riverside California 92521; ⁴Rocky Mountain Biological Laboratory, P.O. Box 519, Crested Butte Colorado 81224; e-mail: kearnsca@rtt.colorado.edu

KEY WORDS: agriculture, ecosystem services, fragmentation, habitat alteration, species invasions

ABSTRACT

The pollination of flowering plants by animals represents a critical ecosystem service of great value to humanity, both monetary and otherwise. However, the need for active conservation of pollination interactions is only now being appreciated. Pollination systems are under increasing threat from anthropogenic sources, including fragmentation of habitat, changes in land use, modern agricultural practices, use of chemicals such as pesticides and herbicides, and invasions of non-native plants and animals. Honeybees, which themselves are non-native pollinators on most continents, and which may harm native bees and other pollinators, are nonetheless critically important for crop pollination. Recent declines in honeybee numbers in the United States and Europe bring home the importance of healthy pollination systems, and the need to further develop native bees and other animals as crop pollinators. The “pollination crisis” that is evident in declines of honeybees and native bees, and in damage to webs of plant-pollinator interaction, may be ameliorated not only by cultivation of a diversity of crop pollinators, but also by changes in habitat use and agricultural practices, species reintroductions and removals, and other means. In addition, ecologists must redouble efforts to study basic aspects of plant-pollinator interactions if optimal

management decisions are to be made for conservation of these interactions in natural and agricultural ecosystems.

INTRODUCTION

To persist on planet Earth, humans depend on “life-support services” provided by biological, geological, and chemical processes in healthy ecosystems. Services such as the cycling of nutrients and regulation of climate are widely recognized. Other such services are less well known, among them biological processes arising from interactions among species, including enhancement of other species’ populations by beneficial biotic agents. The pollination of flowering plants is a prime example: Without pollination by animals, most flowering plants would not reproduce sexually, and humans would lose food and other plant products (22).

One measure of the immense value of ecosystem services is monetary value. A recent estimate places a conservative overall mean value per annum of 33 trillion American dollars on all ecosystem services (40); the component due to pollination services is \$112 billion. Independent estimates placed the annual value of pollination for crop systems at \$20 billion (102) to \$40 billion in the United States alone (159); for global agriculture, the estimated value is \$200 billion (172). Of pollinators other than honeybees, the value to US crop yields may be as high as \$6.7 billion per year (141).

The economic importance of pollination, and its esthetic and ethical values, makes it clear that the conservation of pollination systems is an important priority. In this paper, we describe the ecological and evolutionary nature of plant-pollinator interactions and review evidence that they are increasingly threatened by human activities. We then discuss potential management solutions to ameliorate the “pollination crisis” and highlight areas that call for further research.

THE NATURE OF PLANT-POLLINATOR INTERACTIONS

Modern angiosperms comprise an estimated 250,000 species (81), and most of these—by some estimates over 90% (22, p. 274)—are pollinated by animals, especially insects. Bees alone comprise an estimated 25,000–30,000 species worldwide, all obligate flower visitors (22, 206, 215, 237). The ranks of flies, butterflies and moths, beetles, and other obligate or facultative insect flower visitors surely are several times as large, to which must be added species of birds in several families (35), bats, and small mammals. The number of flower-visiting species worldwide may total nearly 300,000 (141).

Relatively few plant-pollinator interactions are absolutely obligate. Most are more generalized on the part of both plants and animals, and they also vary through time and space (61, 62, 78, 79, 181, 232). For example, the shrub *Lavandula latifolia* in southern Spain is visited by 54 insect taxa from 3 orders, with insects varying substantially in their quality as pollinators (75–77). If added into that is the number of plant species each pollinator visits, the “connectance” of plant and pollinator species in a food web can be high. Jordano (93) reported an average connectance C of about 0.3 for fragments of 36 pollination webs, where C is the realized fraction of the product of n pollinator species and m plant species in the web. C should decline with size of a web, but perhaps not as strongly as previously thought (130, 162).

Recognizing most pollination interactions as being far from obligate fundamentally changes the perception of their conservation. We must abandon the perspective that to lose one plant species is to lose one or more animal species via linked extinction, and vice versa. If the fundamental ecological nature of pollination “interaction webs” is that they are relatively richly connected and shift in time and space, depending in part on the landscape context (20), then the job of conservation biologists is made more subtle and complex.

One major root of generalized interactions is opportunism on the part of both plants and pollinators. To understand this, consider what might be called the fundamental evolutionary nature of pollination. Plants and animal pollinators are mutualists, each benefiting from the other’s presence (13; see also 19, 222). But the mutualism is neither symmetrical nor cooperative. Indeed, pollination derives evolutionarily from relationships that were fully antagonistic (44, 167). The goals of plants and animal pollinators remain distinct—in most cases reproduction on the one hand and food gathering on the other—and this leads to conflict of interest rather than cooperation (83, 233, 239, 240). One place to see this conflict is in the behavior of animals such as bees that “rob” flowers for nectar (87).

The conflict of interest dictates that natural selection will act in divergent ways on plants and pollinators. Pollinators are agents of selection and gene flow from the perspective of plants (30) and are involved in evolutionary events ranging from plant speciation to molding floral phenotype. But floral phenotypes are not simply those that are optimal for the animals (84). Conversely, plants select for features of the animal phenotype (200), but the result is not optimal for the plants. The most basic evolutionary outcome that is common across both plants and pollinators is efficiency of each in exploiting what for each is a valuable or critical resource. One common manifestation is opportunism and flexibility on the part of pollinators toward plants, and vice versa.

To devise the best possible strategies for management, conservation, or restoration of pollination systems, it is essential to have several elements in place. We need excellent knowledge of the natural history of plants and

pollinators. And we need an appreciation for interaction webs and a “Darwinian perspective” on how natural selection is likely to have shaped behavior, morphology, and other aspects of the phenotype of plants and pollinators.

THE POLLINATION CRISIS

Endangered Pollinators and Plants

Disruption of pollination systems, and declines of certain types of pollinators, have been reported on every continent except Antarctica. Although large regions of each continent have not been evaluated, we can assume that disruption is widespread because the causes are widespread phenomena associated with human activities. The overall picture is of a major pollination crisis (22). The causes include habitat fragmentation and other changes in land use, agriculture and grazing, pesticide and herbicide use, and the introduction of non-native species.

Biological Effects of Fragmentation

Many threats to pollination systems stem from fragmentation of once-continuous habitat. Fragmentation creates small populations from larger ones, with attendant problems that include increased genetic drift, inbreeding depression, and (for very small populations) increased risk of extinction from demographic stochasticity (7, 58, 191). Furthermore, fragmentation increases spatial isolation and the amount of edge between undisturbed and disturbed habitat, both of which can harm pollination (133).

If the isolation of fragmented populations becomes greater than the foraging range of pollinators, if the local pollinator population becomes small enough, or if wide-ranging pollinators avoid small populations, the outcome may be reduced pollination services. Limitation of pollen receipt occurs in many plant species. Burd (23) found evidence for pollen limitation for 62% of 258 species surveyed. The degree of limitation typically varies among years, within a season, among sites within a season, and among plants flowering synchronously within a site (54 and references therein).

Population size contributes to pollen limitation. For example, both male function (pollen removal) and female function (fruit set) are functions of population size for three Swedish orchid species (67; see also 110; see 195 for pollinator visitation rates). Some studies of endangered plants have specifically implicated a lack of effective pollinators. Pavlik et al (152) found that seed set of *Oenothera deltoides* ssp. *howellii* was 26% and 37% of maximum in 2 years and suggested scarcity of hawkmoths as a cause; a related species growing in an unfragmented habitat had seed set that was 65% of maximum. Spatial isolation of plants or populations can also play a role. For example,

isolated plants of *Cynoglossum officinale* receive fewer approaches by bumblebees than patches of these plants (108). Percy & Cronk (155) studied an endemic of the island of St. Helena with a total population of 132 adult trees. Pollination is accomplished by small syrphid flies, and pollen delivery declines beyond 50 m; thus, isolated trees are effectively left without pollination.

Pollen limitation does not always imply a dangerous conservation situation. It is often the natural condition due, among other things, to stochasticity in flower visitation (24). Johnson & Bond (92) found widespread pollen limitation in wildflowers in the mountains near Cape Town, South Africa. They attributed this pattern to a general scarcity of pollinators and, in some cases, to lack of floral rewards.

Population size can affect aspects of pollination other than pollen limitation. For example, the composition of the pollinator fauna often differs in flower patches of different size (195, 202). In some cases, such a faunal change may result in higher per-flower visitation rates in small populations (202).

Pollination services are also likely to be affected by density of a plant population, which will sometimes, but not always, covary with population size (114). Thomson (219) and Schmitt (192) reported declines in pollination services at low density for several species in the Asteraceae. Seed set in the desert annual plant *Lesquerella fendleri* depends on the number of conspecifics flowering within 1 m, but not farther away, and behavior of small insect pollinators appears to be the cause (175). Density-related declines in the quality of each pollinator visit (the proportion of conspecific versus foreign pollen delivered) can be more important than parallel declines in the quantity of visits (112, 113, 116).

Interactions of population size, density, and spatial isolation are likely to have even more complex effects on pollination, and these interactions require further study. For example, outcrossing rate is unrelated to population size of an endangered *Salvia* species, but high plant density (in combination with low frequencies of male steriles) promotes outcrossing in hermaphrodites (227). Groom (73) reported that pollen limitation depends on both population size and isolation in a species of *Clarkia*. Of particular concern is an Allee effect—a threshold density, population size, or combination thereof—below which pollinators no longer visit flowers. In a species of *Banksia*, populations below a threshold size produce few or no seeds, presumably in part because of pollen limitation (121; see also 156; for a theoretical approach see 86).

Small plant populations resulting from fragmentation tend to suffer from increased genetic drift and inbreeding depression (58, 228). This may be due to increased geitonogamy, as pollinators may visit a higher proportion of flowers on individual plants, resulting in more self-fertilization (108). Inbreeding depression may explain why small populations of *Ipomopsis aggregata* are more

susceptible to environmental stress and have reduced germination success (80). In general, knowledge of the mating systems of plants often is important for conservation. Self-incompatibility may further compound the dangers of small population size by reducing the availability of suitable mates (27, 49, 122).

Studies of Pollination in Fragments

Recent studies illustrate some of the range of fragmentation-related effects on pollination systems. Most of these effects are clearly deleterious. Aizen & Feinsinger (2, 3), who studied habitat fragmentation in dry thorn forest in Argentina, found fragmentation-related declines in pollination, fruit set, and seed set for most of the 16 plant species examined. For at least two species, frequency and taxon richness of native flower-visitors declined with decreasing fragment size, but visitation by introduced Africanized honey bees tended to compensate for loss of visits by natives in small fragments. Honeybees can be successful in disturbed and fragmented habitats (2, 3, 90, 183), and fragmentation may hasten the spread of Africanized bees (2, 3) and the demise of native pollinators (179, 180).

Spears (203) found that pollen dispersal to neighboring plants is significantly reduced in island populations relative to mainland populations of the same species. Pollinator limitation on islands separated by fewer than 10 km from the mainland may foreshadow the fate of many increasingly isolated mainland plant species. For example, seed set in *Dianthus deltooides* declined in habitat islands even though nectar availability was equivalent to that in an undisturbed "mainland" (90).

A few studies have addressed fragmentation and pollination in tropical areas. Powell & Powell (164) used fragrance baits to determine that male euglossine bees, which are pollinators of many neotropical orchids, would not cross cleared areas as small as 100 m between forest habitats. Allozyme heterozygosity, polymorphism, and effective number of alleles decline in small and isolated populations of the tropical tree *Pithecellobium elegans* (74). In seeming contradiction to this apparent genetic erosion in fragments, pollen dispersal by hawkmoths appears to be substantial for this species and seems easily capable of connecting isolated trees and those in fragments to the rest of the population (32).

The generation of new edges as forests are fragmented will change both abiotic and biotic components of the environment. Murcia (138, 139) divided biotic effects into (a) direct effects that involve changes in the abundance and distribution of species and (b) indirect effects that involve changes in species interactions, including pollination. She detected no consistent changes in pollination levels at a forest edge in Columbia, which suggests that the primary influence of fragmentation is through the creation of smaller populations and the isolation they experience.

The response of insects to fragmentation is poorly understood (50). Bowers (17) studied bumble bee colonization, extinction, and reproduction in subalpine meadows of different sizes. The number and diversity of queens that colonize meadows at the beginning of the summer are positive functions of meadow area, although by mid- to late summer the flower composition of meadows govern species composition and the subsequent reproduction of colonies.

Not all studies have detected negative effects. Stouffer & Bierregaard (209) sampled understory hummingbirds in Amazonian forest before and for nine years after fragmentation. Two species present before isolation did not change in abundance, but one became nearly twice as common, and five were captured only after fragmentation. In contrast to insectivorous birds, the hummingbirds appeared to be plastic in habitat preferences.

Olesen & Jain (144) described how fragmentation can harm not only pollination, but also interactions that plants have with seed dispersers and other mutualists. Loss of these interactions could lead to an extinction vortex with potentially catastrophic consequences for biodiversity. An improved understanding of such effects is critical for conservation (169).

Effects of Agricultural Practices on Wild Pollinators

Humans depend on animal pollination directly or indirectly for about one third of the food they eat (147, 172). Pollination is required for seed production (e.g. alfalfa, clover), to increase seed quality (e.g. sunflower) and number (e.g. caraway), for fruit production and quality (e.g. orchard fruits, melons, tomatoes), to create hybrid seed (e.g. hybrid sunflower), and to increase uniformity in crop ripening (e.g. oilseed rape) (39).

Several features associated with modern agriculture make farms poor habitat for wild bees and other pollinators. Crop monocultures sacrifice floral diversity, and consequently diversity of pollinating insects, over large areas (6, 147, 246). For example, cultivated orchards surrounded by other orchards have significantly fewer bees than orchards surrounded by uncultivated land (193), and the number of bumblebees on crops increases with proximity to natural habitats (246). Chemical fertilizers, pesticides, and herbicides harm pollinators. In addition, marginal land is increasingly cultivated (52, 101, 103, 147, 225 and references therein), resulting in (a) loss of wild vegetation to support pollinators, (b) fewer areas where bees can nest, (c) fewer larval host plants for butterflies, and (d) less-varied microhabitats for egg laying and larval development (52, 246). For example, since 1938, Britain has lost 30% of its hedgerow habitats, which provide floral resources and nesting sites for wild bees at the margins of cultivated fields (146).

Elimination of many native pollinators is an unappreciated price that has been paid for increased food production over the last 50 years (172, 224, 225). These

pollinators are lost to adjacent natural ecosystems and to crop pollination as well. Although honeybees have long been considered the most important crop pollinators (references in 10, 147), wild pollinators are also important (165) and can be managed to provide “free” services (10, 39, 165).

Shortages of bees to pollinate crops have now been predicted in both Europe and the United States (146, 224). At least 264 crop species from 60 families are grown in the European Union, 84% of which are believed to be dependent on insect pollination (244). The best evidence for declines in bee populations comes from Europe (38, 143, 147, 172, 246), although similar losses have occurred elsewhere.

Damage is not restricted to agricultural situations in industrialized countries. Vinson et al (229) documented disruption in pollination systems following the clearing of tropical dry forest in Costa Rica to provide land for grazing and agriculture. Where livestock are raised, native grasses are commonly replaced with introduced forage grass, which burns more readily and hotly than native grasses. Fires from private lands spread to adjacent forest reserves, threatening native plants and the insects and bats that pollinate most of them. The direct effect of fire is not the only problem. Some specific relationships exist between anthophorid bees such as *Centris* and oil plants of the family Malphiaceae. Several species of *Centris* depend on finding dead wood with holes formed by wood-boring insects, a resource that disappears when forests are cleared. Many oil-producing plants burn, and those that survive produce less oil. Bees in the dry forests appear to be decreasing in both numbers and diversity, and trees that historically provided bee resources, and depended on bees for outcrossing, are disappearing.

Grazing

Grazing threatens pollinators through removal of food resources, destruction of underground nests and potential nesting sites, and other more subtle mechanisms (70, 96, 211).

Sugden (211) studied sheep grazing practices in California and the effects on pollinators of an endemic vetch (*Astragalus monoensis*) and found evidence of nest destruction, pollinator food removal by sheep, and direct trampling of bees. Bees at risk included *Anthidium*, *Anthophora*, *Bombus*, *Callanthidium*, *Colletes*, *Hoplitis*, and *Osmia*. Another example of removal of food resources by grazing is the loss of willow shrubs (*Salix* spp.) due to cattle along riparian areas. These willows are important browse for livestock (186) and provide nectar and pollen for spring-emerging bumblebee queens and other pollinators; their loss may harm the pollinators and, in turn, other species of plants that flower later in the summer.

Pesticides

Pesticides pose a major threat to pollinators (9). Ironically, the greatest use of pesticides is on crop plants where pollinators are most often limited. Pollinators also are harmed by pesticide application in grasslands (18, 154, 215), forests, (101), urban areas (103), and even tourist resorts (47). An increasing awareness of environmental risks has helped reduce pollinator poisonings in industrialized nations (103), but pesticide-induced declines in bee abundance are still being reported from developing countries (43).

Bee poisoning from insecticides first became a problem in the United States in the 1870s (91), but advances in agricultural technology and elaboration of new chemicals exacerbated the problem after World War II (5, 91). Poisoning of honeybees (on which most attention has been focused) can result in direct mortality, abnormal communication dances, inability to fly, and displacement of queens (91). Foraging honeybees can contaminate the hive with pesticides or other pollutants. Pesticides, arsenic, cadmium, PCBs, fluorides, heavy metals, and radionucleotides (after the 1986 Chernobyl accident) have all been reported in contaminated honey or pollen (103).

In the 1970s, Kevan (98–100) cautioned about the disruptive effects of pesticides on native pollinators, and his predictions have been borne out. The best example is a long-term study conducted in Eastern Canada (99, 101, 103, 104, 106, 161). From 1969 until 1978, spruce budworm was controlled by aerial spraying of Fenitrothion, an organophosphate that is highly toxic to bees. Commercial blueberry production in the region largely depended on pollination by as many as 70 species of native insects. Blueberry crops failed in 1970 and subsequent years (102). Populations of bumblebees and andrenid and halictid bees declined in blueberry fields near sprayed forests (99), and reproduction of native plants was depressed (218, 221). Native bees showed steady signs of recovery after Fenitrothion was replaced with a less harmful insecticide (101).

In the western United States, broad-spectrum insecticides are used to control grasshoppers on rangelands (215). Spraying occurs during the flowering of a number of threatened or endangered endemic plants (18) and coincides with the foraging period of most native bees (154). Spraying is prohibited in a 3-mile radius around points where listed plants are known to occur, but the 3-mile figure is arbitrary because little is known about flight distances of the pollinators (154). Some of these listed species appear to have pollinator-limited seed production (63), and their persistence will be related to successful pollination (194, 215).

Herbicides

Herbicide use affects pollinators by reducing the availability of nectar plants (47, 100). In some circumstances, herbicides appear to have a greater effect

than insecticides on wild bee populations (11,47). Herbicide spraying and mechanical weed control in alfalfa fields can reduce nectar sources for wild bees. The magnitude of the effect for each species is related to the length of its seasonal flight period. Many bees have a flight period that extends beyond the availability of alfalfa flowers. Some of these bee populations show massive declines due to the lack of suitable nesting sites and alternative food plants (11).

Honeybee Declines

More than 9000 years ago, humans realized they could harvest honey from the stores of some bees (69). Humans have taken honeybees with them as they settled new regions of the world (21). Honeybees have been domesticated and naturalized in temperate areas of Australia, North America, and South America for centuries (before 1641 in North America) (196), whereas extensive naturalization in tropical regions is much more recent (183). Although *Apis mellifera* is native to western Asia, it is not widely naturalized in other parts of Asia, where five other species of *Apis* naturally occur (37, 183).

Today, bee products are still valuable, but the value of crop pollination is far greater (22; references in 10). Honeybees, which are generalists and will pollinate many crops, are easily managed and transported (147). Some suggest the annual value of honeybee pollinated crops in the United States alone is as high as \$10 billion (235; see also 201, 224).

Recently, honeybees have been declining. More than 20% of the cultivated honeybee colonies in the United States have been lost since 1990 (85,235), along with most feral honeybees (235). The number of commercially managed colonies has declined from a peak of 5.9 million in the 1940s to 4.3 million in 1985 and 2.7 million in 1995 (85). Declines are severe in some regions. For example, in 1994, California almond growers had to import honeybees from as far away as Florida (235). The European community supports an estimated 7.5 million managed honeybee colonies (244, 245), and these are believed to have been declining since 1985 (245).

Two parasitic mites, *Varroa jacobsoni* and *Acarapsis woodi*, have been particularly damaging to honeybees. *Varroa* spread from its original host, the Asiatic honeybee (*Apis cerana*), when *A. mellifera* was introduced to Asia (57). The mites had spread from Asia to Europe by 1950, to North Africa by 1970, to South America by 1971, and to North America by 1987 (136). A bee infected by *Varroa* loses protein to the parasite, resulting in lowered life expectancy. Also, bacteria penetrate holes in the exoskeleton formed by the mites (174). Existence of *A. woodi*, the tracheal mite, was first documented in England in 1921; subsequently it spread to continental Europe, Asia, Africa, South America, and North America (42, 57). Entire bee colonies become infected, resulting in decreased brood production, decreased honey production, and high winter

mortality (48). Beekeepers can attempt to control both mites with chemicals, but *Varroa* mites are beginning to exhibit resistance (236). Treatment can be costly, and chemical residues may appear in honey. New control techniques are being developed, but the difficulty of mite control is causing a decline in beekeeping, particularly among hobbyists (103, 235).

Africanized honeybees also are implicated in honeybee decline in the Americas. The term Africanized has been used to describe hybrids between honeybees of European descent and African subspecies *A. mellifera scutellata* (173). Taylor (214) suggested that the term neotropical African bees be used for the feral colonies in South and Central America that still retain the African phenotype distinguishable by morphology, behavior, and genetics, and that the term Africanized bees be used to refer to bees found primarily in apiaries that show clear evidence of hybridization. The failure to make these distinctions has led to differing predictions about the spread of the bees (214). African queens were released accidentally in Brazil in 1956 (136) and rapidly dominated colonies of European descent. The bees became established in the United States in 1990 (22). The predominately African phenotype may be restricted to the warmer climate of the southern United States, but the variable hybrid Africanized phenotypes may be able to survive farther north (214). Neotropical African bees display several features that make them undesirable for apiculture. They swarm when colonies are relatively small and have little honey, and they leave an area when environmental conditions become unfavorable (64). Furthermore, their reputation for aggressive behavior is responsible for negative public attitudes and a decline in beekeeping (22, 34, 201).

Non-Native Pollinators

The introduction of non-native pollinators has the potential to harm native pollination systems. For example, fig wasps were introduced to California in 1899, at which point non-native trees that had been grown there for decades began to produce fruits (51). Because of the introduction of their wasp pollinators, some fig species are now weedy pests in parts of the continental United States, Hawaii, and New Zealand (68, 132). The introduction of bumblebees into areas sometimes have negative results. Non-native *Bombus terrestris* were brought to Japan to pollinate greenhouse tomatoes but soon escaped and became naturalized (I Washitani, personal communication). Because of their aggressive nature, queens are able to take over the hives of native bumblebees by killing the queen, and ecologists fear serious declines in native bumblebee species. Queens of the native Japanese *Bombus diversus* are important pollinators of at least one endangered plant, *Primula sieboldii* (234), and cannot be replaced by *B. terrestris*. *B. terrestris* has also invaded parts of Israel in recent decades, expropriating nectar resources to the apparent detriment of native bees

(46a). *Xylocopa* carpenter bees are pollinators of some plants but are also well known as nectar robbers (87). Little is known about the impact of this bee on native species of flowers or pollinators in Hawaii, where it was introduced (82).

By far the most significant introduction of non-native pollinators involves honeybees, whose movement by humans to all areas of the globe can be considered a major, uncontrolled ecological experiment. Honeybees in some cases might benefit wildflowers by excluding native pollinators from crops (245), but they are often poor pollinators of crops and native flowers compared with native insects (10, 115, 147, 148, 165, 172, 184, 224, 239). Furthermore, honeybee colonies require prodigious amounts of pollen and nectar, and worker bees fly long distances and recruit to rich floral resources (21, 183). Thus, honeybees may compete with native pollinators for resources, leading to reduced species diversity of pollinators. Honeybees also are likely to affect the reproduction of native plants, perhaps even facilitating the spread of weedy non-native plants (4, 8, 82, 128, 188; see also 26). Whether or not honeybees aid in the spread of introduced plants, the presence of these plants may disrupt natural pollination systems because native pollinators sometimes prefer them at the expense of native plants (230).

Competition with honeybees has been implicated in the decline of buprestid beetles in western Australia (109). These jewel beetles are important pollinators in arid mallee scrub vegetation. Sugden & Pyke (212) demonstrated competition by introducing honeybees into an alpine area of Australia and examining the nesting and reproductive success of a generalist native bee. Honeybees remove as much as half of all the available nectar from flowers of the Australian bottlebrush, *Callistemon rugulosus*, and New Holland honeyeaters respond by visiting individual flowers less frequently and expanding their feeding territories (149, 150). Honeybees visit many other Australian plants and on some species remove over 90% of the available resources (151). Roubik et al (176–178, 182, 183, 185) studied competition between African honeybees and native pollinators in South and Central America. In French Guiana, African honeybees are common visitors to *Mimosa pudica* (183). Patches dominated by honeybees had the lowest levels of seed and fruit production, whereas highest levels occurred in patches visited by native *Melipona* bees. Honeybees have been increasing in moderately disturbed, mixed forest-savanna habitats (from 20% of visitors in 1977 to 99% of visitors in 1994), which suggests that they are displacing native insects. Honeybees were introduced onto Santa Cruz Island, off the coast of California, in the 1880s and can now be found foraging on more than one third of the island's plant species (223, 238). Removal of honeybee colonies from the eastern half of the island over the past few years suggests an inverse relationship between honeybee abundance and native bee

abundance. Experiments in old field in New York state show that the native megachilid bee *Osmia pumila* suffers reduced brood cell production and pupal mass, and increased brood parasitism in the presence of honeybees (K. Goodall, unpublished).

The hypothesis of competition is not supported by all studies. Sugden et al (213) reviewed 24 studies conducted on four continents and three islands; 16 detected competition under some conditions whereas 8 produced ambiguous results. Although Africanized honeybees reached the neotropics two decades ago and the foraging behavior of native bees changes when honeybees are present, there is no strong evidence of declines in native bee populations (25). Perhaps this is unsurprising: Where honeybees monopolize a rich resource, native species may shift to other flowers and there may be no effect on their population size (150, 183, 190). Also, effects of competition are difficult to detect, if they occur, against the background of natural variation in pollination systems (25, 183). The idea that honeybees automatically compete with natives is probably naive (183), and more studies, including ones of longer duration, are needed.

POTENTIAL MANAGEMENT SOLUTIONS

Conservation of Habitats and Pollinators

Conservation biology is undergoing a paradigm shift away from single-species conservation efforts and toward habitat, ecosystem, and regional efforts. Pollinators should benefit from this change, because the pollinators of many plant species are not yet identified and stand to gain protection from blanket conservation efforts. Also, it is difficult to convince the public to devote resources to protecting small insect pollinators whose aesthetic beauty is not obvious to the unaided eye. The broad context of habitat- or ecosystem-level conservation efforts is especially appropriate for pollination systems because of the web of interactions that links plant species via pollinators (216, 232).

Studies of several systems demonstrate why an ecosystem-based conservation strategy is valuable. A rare orchid in the western United States, *Spiranthes diluvialis*, requires pollinators, so management plans must encompass the maintenance of bumblebees, which may be at risk from insecticide spraying on public rangeland (197). The habitat must also be managed for appropriate nest sites for bumblebees, and for floral diversity to provide nectar (the orchid produces none) and pollen for the whole flight season of bumblebees (199). Petit & Pors (158) calculated the carrying capacity for nectar-feeding bats on the island of Curaçao by using the daily availability of flowers on three species of columnar cacti. They estimated the carrying capacity for one bat species at 1200, about 300 more than the actual population, and suggested that removal

of native vegetation on the island should be strictly regulated to prevent further decline. Cropper & Calder (45) attributed the lack of seed set of the rare and endangered Australian orchid *Thelymitra epipactoides* to the absence of pollinators and suggested elimination of natural fire as the root cause. Burning stimulates flowering in many coastal heathland species, which helps to maintain high pollinator species diversity. Kwak et al (118) pointed out the value of other plant species in attracting bumblebees to small populations of the rare Dutch plant *Phyteuma nigrum*.

The dependence of wild pollinator populations on appropriate habitat is increasingly recognized. A study of margins of agricultural fields (119) pointed out that small areas with flowering plants can be very effective at attracting and maintaining pollinator populations, including Syrphidae and other Diptera. Habitat could be managed to encourage bumblebee and honeybee populations by providing a seasonal succession of suitable forage plants, protecting them from pesticides and herbicides and providing for long-term set-aside of fields (38, 145; see also 242). The last recommendation makes sense because butterflies and bumblebees tend to prefer flowers of perennials and because ground-nesting bees avoid recently disturbed areas (38). Such a policy could also benefit insect species that are not crop pollinators, e.g., satyrid butterflies (53).

Conservation of bee habitat may be the best means of reversing declines in pollinator populations (172). In many parts of the world this may mean conservation of human-made habitats, some of which prove to be good substitutes for threatened or destroyed natural habitats (47, 107, 242). Many bee species have colonized restored areas along the Rhine River. Levees can provide prime bee habitat, especially when built of sand and gravel and managed for high floral diversity (107). Day (47) argued that as technology becomes more important and farming starts to decline in Europe, hedgerows, pastures, and woodlands should be regenerated. Disturbed urban areas may also be favorable for some bee communities (189), although multiple types of habitat may be required to satisfy both foraging and nesting requirements (241).

Some pollinators only need a relatively small patch of habitat near their host plants, but others require large areas. In Santa Rosa National Park in Costa Rica, there are at least 40 species of sphingid moths, which pollinate at least 50 plant species as adults and which live for one generation in the park during the beginning of the rainy season before moving to other parts of the country for the rest of the year (89). For these and other migratory pollinators, conservation efforts can require large geographical areas and even international cooperation. Perhaps the most extreme examples are migrants such as hummingbirds, butterflies, and moths, which may be important pollinators along migratory routes extending for thousands of kilometers (12, 28, 71, 231).

Maintenance of Populations and Species in the Absence of Pollinators

Relatively few examples exist of the absolute loss of pollinators, but this may reflect only our ignorance. Steiner (204) reported the loss of a specialized oil-collecting pollinator of a rare South African shrub, although subsequent work (205) led to discovery of a population where the predicted specialist pollinator was still present. Sipes & Tepedino (198, p. 164) suggested that one interpretation of the low visitation and fruit set to a rare plant from the western United States is that the original pollinator “is no longer consistently found within the plants’ distribution.” Lord (125) described a New Zealand liane that has lost its bat pollinator.

One effort that may, at least in the short term, prove fruitful for conservation is hand pollination of plants that have lost natural pollinators. For example, *Trifolium reflexum*, a prairie species threatened by loss of habitat, was brought into cultivation at the Chicago Botanic Garden, where hand pollination yielded thousands of seeds for additional restoration efforts (208). Hand pollination has also been used for two Hawaiian species of *Brighamia*, whose few remaining individuals have apparently lost their native pollinators (22), and for an endangered orchid in Illinois (168).

Biosphere 2, an experiment in which a small human population was sealed in a (mostly) closed environment for 2 years, included a diversity of plants. All pollinators quickly went extinct so that most plant species “had no future beyond the lifetime of individuals already present” (33). One conclusion is that maintenance of normal plant-pollinator relationships is difficult and that people in such circumstances in the future should be prepared for hand-pollinating.

Another possible solution is the intentional introduction of exotic pollinators, although there are risks (10, 51, 101, 105). The first known example was the introduction of bumblebees to pollinate red clover in New Zealand (51, 65). More recently, weevils were introduced to pollinate oil palms in Malaysia (101), providing services valued at \$3 million per year (72, 187).

Changed Agricultural Practices and Uses of Pesticides and Herbicides

In the United States alone, crop production is reduced by about 8000 species of insects, 2000 species of weeds, 160 types of bacteria, 250 types of viruses, and 8000 species of pathogenic fungi (9). Pesticides and herbicides seem an attractive solution because they can rapidly reduce numbers of problem organisms. However, new chemicals must be continually developed as pests evolve resistance and for other reasons (9). One alternative is to move to more labor-intensive control methods that are more “friendly” to pollinators. For example,

some USDA studies comparing organic farms and nearby farms using pesticides showed similar crop yields (9). The organic farms controlled pests in ways that encouraged natural predators of pests and created more favorable habitats for pollinators.

There is an increasing emphasis on preventing pollinator loss due to application of crop pesticides. Toxicity levels of pesticides to honeybees are generally known (103), but this has not been useful in determining the effects on other bees (142). Toxicity is in part related to surface-to-volume ratio (91), so that bumblebees may be more tolerant, and small solitary bees more susceptible, than honeybees. In addition, details of pesticide use (such as timing, method of application, and formulation) can affect toxicity (43, 142). Crops can be sprayed before or after flowering to minimize the chances of harming pollinators (66). However, leafcutter bees may collect contaminated leaf tissue for nest construction even when crops are not in flower (142). Timing of application within the day can also be critical. Although honeybees are not active at night, some bees, such as *Nomia*, rest in crop fields at night where they would be susceptible to night spraying (142). Bees such as *Apis* and *Nomia* forage as far as 13 km from the nest (142), so spraying may affect bees that nest far from fields. Honeybee apiaries can be either moved or closed-up during pesticide application, but native bees are not as fortunate. Compounds such as benzaldehyde, propionic anhydride, and some amines may prove useful in repelling bees from fields during pesticide application (142). Bran-baits instead of pesticide spraying could be used to kill grasshoppers in rangelands, thereby potentially reducing pollinator mortality (153).

Few studies have systematically documented declines of bees other than honeybees (but see 99, 103 and references therein). Documentation can be difficult because baseline data are generally unavailable and often the importance of non-*Apis* bees is poorly understood (142). However, enough is known about pesticide problems that much can be done to reduce pollinator losses (103). Kevan (103) suggested regulation and certification for pesticide users. In many countries, regulations are in place but violations carry minimal penalties (103).

Reintroductions of Plants and Pollinators

Reintroduction of endangered plants is still relatively uncommon (60). No plant reintroduction to date appears to have been stimulated by the need to support pollinator populations, although existing pollinators may have benefited. Maunder's (131) paper on plant reintroduction does not mention pollinators, nor does that by Falk et al (60).

One potential problem of reintroducing a plant species into an area is that during its absence some native pollinators may have vanished. This loss would be most serious if the plant had a single pollinator species, but such species

appear to be in the minority, and it is common for a plant to have multiple, sometimes very numerous, pollinators (232). Given the variability among years that can be observed in pollinator populations (e.g. 31, 79, 95, 127, 157), multiple pollinators may often be necessary for plant persistence (232).

Hawaii provides one example of an introduction that inadvertently filled the role of a recently extinct pollinator. Cox (41) described the pollination of *Freycinetia arborea*, the indigenous ieie vine, by *Zosterops japonica* (Japanese White-eye, introduced in 1929). Museum specimens of three native birds, two extinct and one endangered, carried pollen grains from the plant, indicating that they were among the original pollinators. Lammers et al (120) reported that White-eyes also visit flowers of an endemic lobelioid, *Clermontia arborescen*. Not all Hawaiian plants have been so lucky; some have gone extinct whereas others are very rare.

Removal of Alien Pollinators

Animals have been intentionally introduced because of their role as pollinators (e.g. honeybees, the alfalfa leafcutter bee). Some intentional introductions involve animals that pollinate but were not introduced for that reason (e.g. *Zosterops* in Hawaii, possums in New Zealand) and some unintentional introductions involve pollinators (e.g. cabbage butterflies, fig wasps). In only a few cases have there been calls for the removal of introduced pollinators. The European bumblebees that were introduced to Japan as pollinators of greenhouse crops escaped to establish feral populations. An effort to eradicate them is underway (M Ono, personal communication). *B. terrestris* was also introduced in about 1992 to Tasmania, where an attempt to eradicate it has had little success (163).

Domestication of Wild Bees and Other Pollinators

Research on non-*Apis* bees as crop pollinators has a long history (15, 224), but it recently has achieved new significance (220, 243). As early as the 1980s, concerns were raised about the need for an increased diversity of pollinators for agriculture in North America (148, 172). At least 50 native bee species have been cultivated experimentally or commercially (43, 172, 224, 225). Parker et al (148) also discussed the use of dipterans as possible crop pollinators.

A few success stories illustrate the potential for non-*Apis* bees as pollinators. The leafcutter bee (*Megachile rotundata*) was introduced from Asia into North America and is the primary pollinator of plants grown to produce alfalfa seed (171, 220). In 1977, *Osmia cornifrons* was introduced from Japan as a pollinator of apples; it has now been distributed to 23 states and 2 Canadian provinces (148; see also 172, 225). In the tomato industry, bumblebees can replace humans equipped with electric vibrators (the flowers require "buzz pollination" to release pollen) or sprayers with synthetic plant hormones to induce

fruit production (124, 148, 172). The bumblebee business originated in The Netherlands about a decade ago and has now spread as far as North America and Japan (124, 148, 172).

Legal Protection

Nearly 25% of the planet's vascular plant species may become extinct within the next 50 years (170), and 22% of the species in the United States is currently of conservation concern (59). The situation for most pollinators appears less bleak because the numbers are smaller, but this may only reflect poorer knowledge of them. Both plants and pollinators can be afforded legal protection through the Endangered Species Act in the United States and internationally via listing in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). In the United States, only 390 of the 639 species of flowering plants afforded protection by the Endangered Species Act had recovery plans as of December 1997 (<http://www.fws.gov/~r9endspp/pltl1data.html>), and only 16 species of butterflies, 1 species of fly, 1 species of moth, and 2 species of skippers (Lepidoptera) were included in the list as endangered or threatened (<http://www.fws.gov/~r9endspp/invdta.html#Insects>) as of that date. Three vertebrate pollinators, two flying fox species and the lesser long-nosed bat (*Lep-tonycteris curasoeae*), were also listed as of December 1997. The International Union for Conservation of Nature and Natural Resources (IUCN) now lists 165 genera of vertebrate pollinators (including 186 species) of conservation concern (140), which suggests a need for legal protection for many more.

Public Education

Education efforts have helped bring publicity to bee conservation efforts in Europe, particularly for bumblebees. The Watch Trust for Environmental Education engaged thousands of volunteers, mostly children, to document the abundance and distribution of *Bombus* species and to provide information on preferred plant species (117, 146). The success of this survey inspired a similar program in The Netherlands.

In 1995, The Arizona-Sonora Desert Museum launched the Forgotten Pollinators Campaign. The focus was to draw attention to the impending pollination crisis. The campaign included publication of a book (22), media campaigns, a research program conducted by volunteers, development of pollinator gardens at the museum, and other efforts to increase public awareness of the importance of pollinator conservation.

PRIORITIES FOR FURTHER RESEARCH

In virtually all cases, biologists must provide scientific information for conservation decisions based on less-than-perfect knowledge. The best approach is

to base scientific input on the consensus of experts; this is vastly preferable to no scientific input at all or to that of a small minority (55). At the same time, it is important for pollination biologists to map out a research program for filling major gaps in our knowledge, as we attempt to do here.

The Ecology of Animal Pollinators

Typical ecosystems at intermediate latitudes harbor as many as several hundred pollinating insect species, most belonging to Hymenoptera, Lepidoptera, Diptera, and Coleoptera (79, 111, 134, 157, 210, 247). The vast majority of hymenopteran pollinators are solitary bees (237). Compared with our understanding of social bees, we still have much to learn about the nesting biology, demography, and trophic ecology of most solitary bees and about the composition of local species assemblages (137, 215). Relative abundances of given species of solitary bees fluctuate spatially and temporally (31, 157), and we need to understand how this relates to floral resources (215). We also need to learn more about the degree of specialization of individual bee species and the degree to which even specialists may use other plant species (31, 46). The picture for other insect orders is further complicated by the fact that larvae may require food plants that differ from those of adults. We need to learn how to manage landscapes that will support the entire life cycle of such species (22, 14). Our knowledge of larval ecology is best for the Lepidoptera because of the intense interest of naturalists in butterflies (56). More effort needs to be expended in learning comparable information about dipteran and coleopteran life cycles and larval diets. The role of flies as pollinators in many ecosystems seems to have been underestimated until recently (94, 157, 226, 247).

Links Between Pollination and Plant Population Dynamics

The diversity of pollinators is matched by local diversity of plant species and temporal and spatial variation in species composition. For example, Tepedino & Stanton (217) reported substantial year-to-year variation in relative abundances and phenologies of different flowers in a shortgrass prairie in Wyoming (see also 88, 166). Thus, a pollinator foraging for floral reward experiences a complex and fluctuating marketplace. It is important to characterize variation in floral abundance more carefully and to study how pollination contributes to it. Ecologists have assumed that pollination plays an important role in plant population dynamics, but there is virtually no empirical evidence for it. We do know that pollination is often limiting to seed production (23), although resources (207) or both pollination and resources simultaneously (29, 135) can also be limiting. However, we need more experimental manipulations of seed input, seedling establishment, and other stages of the life cycle with measurement of subsequent changes (if any) in plant population size and structure (1, 126, 129).

In particular, it would be useful to design such studies so they help us to predict how reduction in pollination services will influence the demography of plant species that are threatened because of fragmentation of other anthropogenic insults.

The Nature of Interaction Webs

Pimm (160) distinguished four aspects of ecological stability, one of which is resilience—the degree to which an ecosystem resists further change following initial change. Pollination webs are threatened with the loss of component species and addition of non-natives. The substantial connectance of pollination webs makes us suspect that such changes will elicit additional ones, perhaps even cascades of extinction. To our knowledge, nobody has modeled resilience (or other aspects of stability) specifically for mutualistic interactions such as those of plants and pollinators, much less studied resilience of such systems empirically.

CONCLUDING THOUGHTS

The natural history knowledge of pollination gained over the last several centuries shows that animal-mediated pollination is essential for the sexual reproduction of most higher plants. Although many plants are iteroparous, with multiple opportunities for sexual reproduction, spread by clonal propagation or other asexual means or having a dormant seed stage, these life-history features cannot compensate in the long term for a chronic loss of pollination services (16). A reduction in plant fecundity is of clear concern for agroecosystems but equally problematical for natural ecosystems. There is indeed a strong argument to be made that pollination interactions are keystones in both human-managed and natural terrestrial ecosystems (102).

In spite of centuries of study, our understanding of interactions between plants and animal pollinators is far from complete. Appreciating this was our motivation for stressing that continued research is essential to the long-term conservation of pollination systems. At the same time, we agree with others in political and scientific circles who urge ecologists to become more active in educating those around them about issues in conservation biology. The evidence on multiple fronts is sufficiently alarming to conclude that there is an ongoing and pending ecological crisis in pollination systems. Although there are dangers in sounding the alarm for a pollination crisis, and hurdles to be overcome in explaining the issues to a wider audience, the alternatives hold far greater risks.

Our understanding of the keystone role that pollinators can play in ecosystems around the world, and the risks faced by both pollinators and the plants

they visit, has increased greatly during the past few decades. Research on endangered plants, including rehabilitation and reintroduction programs, is more likely now than in the past to include consideration of breeding systems and the potential need for pollinators in management plans (97, 123). The conservation of insects and their habitats is now a topic for discussion in the scientific literature (36). A decade ago, Feinsinger (62) found only two papers that clearly related conservation and animal-flower interactions; now these topics are written about frequently, as our review shows. Much progress has been made since Kevan's plea arising from concern about the damage to pollinators from pesticide and herbicide use in Canada (100). The most encouraging progress is that we now recognize much more clearly what problems exist and what we need to know to solve them.

At the same time, many challenges lie ahead. We must redouble our research efforts on basic aspects of pollination systems at a time when it is difficult to obtain financial support for work that lacks immediate management applications. The pace of change in ecosystems and growth of threats to pollination systems promise to increase in the future. We face accelerated alteration of habitat by a growing human population, linked with accelerated invasion of non-native species, and the prospect of global climate change, which threatens to decouple plants and pollinators phenologically and ecologically (166). Although the challenges are daunting, they must be met with our most determined efforts as ecologists and citizens.

Visit the *Annual Reviews* home page at
<http://www.AnnualReviews.org>

Literature Cited

1. Ackerman JD, Sabat A, Zimmerman JK. 1996. Seedling establishment in an epiphytic orchid: an experimental study of seed limitation. *Oecologia* 106:192–98
2. Aizen MA, Feinsinger P. 1994. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology* 75:330–51
3. Aizen MA, Feinsinger P. 1994. Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine "Chaco Serrano." *Ecol. Appl.* 4:378–92
4. Allen RB, Wilson JB. 1992. Fruit and seed production in *Berberis darwinii* Hook., a shrub recently naturalized in New Zealand. *NZ J. Bot.* 30:45–55
- 4a. Allen-Wardell G, Bernhardt P, Bitner R, Burques A, Buchmann S, Cane J, et al. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conserv. Biol.* 12:8–17
5. Anderson LD, Atkins EL. 1968. Pesticide usage in relation to beekeeping. *Annu. Rev. Entomol.* 13:213–38
6. Banaszak J. 1996. Ecological bases of conservation of wild bees. See Ref. 130a, pp. 55–62
7. Barrett SCH, Kohn JR. 1991. Genetic and evolutionary consequences of small population size in plants: implications for conservation. In *Genetics and Conservation of Rare Plants*, ed. DA Falk, KE Holsinger, pp. 3–30. New York: Oxford Univ. Press
8. Barthell JF, Randall JM, Thorp RW, Wenner AM. 1994. Invader assisted invasion: pollination of star-thistle by

- feral honey bees in island and mainland ecosystems. *Bull. Ecol. Soc. Am.* 75:10 (Abstr.)
9. Batra SWT. 1981. Biological control in agroecosystems. *Science* 215:134–39
 10. Batra SWT. 1995. Bees and pollination in our changing environment. *Apidologie* 26:361–70
 11. Benedek P. 1972. Possible indirect effect of weed control on population changes of wild bees pollinating lucerne. *Acta Phytopathol. Acad. Sci. Hung.* 7:267–78
 12. Bertin RI. 1982. The ruby-throated hummingbird and its major food plants: ranges, flowering phenology, and migration. *Can. J. Zool.* 60:210–19
 13. Bertin RI. 1989. Pollination biology. In *Plant-Animal Interaction*, ed. WG Abrahamson, pp. 23–86. New York: McGraw-Hill
 14. Blair RB, Launer AE. 1997. Butterfly species diversity and human land use: species assemblages along an urban gradient. *Biol. Conserv.* 80:113–25
 15. Bohart GE. 1972. Management of wild bees for the pollination of crops. *Annu. Rev. Entomol.* 17:287–312
 16. Bond WJ. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philos. Trans. R. Soc. London Ser. B* 344:83–90
 17. Bowers MA. 1985. Bumble bee colonization, extinction, and reproduction in subalpine meadows in northeastern Utah. *Ecology* 66:914–27
 18. Bowlin RW, Tepedino VJ, Griswold TL. 1993. The reproductive biology of *Eriogonum pelinophilum* (Polygonaceae). See Ref. 199a, pp. 296–302
 19. Bronstein JL. 1994. Conditional outcomes in mutualistic interactions. *Trends Ecol. Evol.* 9:214–17
 20. Bronstein JL. 1995. The plant-pollinator landscape. In *Mosaic Landscapes and Ecological Processes*, ed. L Hansson, L Fahrig, G Merriam, pp. 257–88. London: Chapman & Hall
 21. Buchmann SL. 1996. Competition between honey bees and native bees in the Sonoran Desert and global bee conservation issues. See Ref. 130a, pp. 125–42
 22. Buchmann SL, Nabhan GP. 1996. *The Forgotten Pollinators*. Washington, DC: Island. 292 pp.
 23. Burd M. 1994. Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. *Bot. Rev.* 60:83–139
 24. Burd M. 1995. Ovule packaging in stochastic pollination and fertilization environments. *Evolution* 49:100–9
 25. Butz Huryn VM. 1997. Ecological impacts of introduced honeybees. *Q. Rev. Biol.* 72:275–97
 26. Butz Huryn VM, Moller H. 1995. An assessment of the contribution of honey bees (*Apis mellifera*) to weed reproduction in New Zealand protected natural areas. *NZ J. Ecol.* 19:111–22
 27. Byers DL. 1995. Pollen quantity and quality as explanations for low seed set in small populations exemplified by *Eupatorium* (Asteraceae). *Am. J. Bot.* 82:1000–6
 28. Calder WA. 1987. Southbound through Colorado: migration of rufous hummingbirds. *Natl. Geogr. Res.* 3:40–51
 29. Campbell DR, Halama KJ. 1993. Resource and pollen limitations to lifetime seed production in a natural plant population. *Ecology* 74:1043–51
 30. Campbell DR, Waser NM, Meléndez-Ackerman EJ. 1997. Analyzing pollinator-mediated selection in a plant hybrid zone: hummingbird visitation patterns on three spatial scales. *Am. Nat.* 149:295–315
 31. Cane JH, Payne JA. 1993. Regional, annual, and seasonal variation in pollinator guilds: Intrinsic traits of bees (Hymenoptera: Apoidea) underlie their patterns of abundance at *Vaccinium ashei* (Ericaceae). *Ann. Entomol. Soc. Am.* 86: 577–88
 32. Chase MR, Moller C, Kessell R, Bawa KS. 1996. Distant gene flow in tropical trees. *Nature* 383:398–99
 33. Cohen JE, Tilman D. 1996. Biosphere 2 and biodiversity: the lessons so far. *Science* 274:1150–51
 34. Collins AM. 1988. Genetics of honeybee colony defense. See Ref. 143a, pp. 110–17
 35. Collins BG, Paton DC. 1989. Consequences of differences in body mass, wing length and leg morphology for nectar-feeding birds. *Aust. J. Ecol.* 14: 269–89
 36. Collins NM, Thomas JA, eds. 1989. *The Conservation of Insects and Their Habitats*. London: Academic
 37. Connor LJ, Rinderer T, Sylvester HA, Wongsiri S, eds. 1993. *Asian Apiculture. Proc. First Int. Conf. Asian Honey Bees and Bee Mites*. Cheshire, CT: Wicwas
 38. Corbet SA. 1995. Insects, plants and succession: advantages of long-term set-aside. *Agric. Ecosyst. Environ.* 53:201–17
 39. Corbet SA, Williams IH, Osborne JL. 1991. Bees and the pollination of crops

- and wild flowers in the European Community. *Bee World* 72:47–59
40. Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, et al. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387:253–60
 41. Cox PA. 1983. Extinction of the Hawaiian avifauna resulted in a change of pollinators for the ieie, *Freycinetia arborea*. *Oikos* 41:195–99
 42. Crane E. 1988. Africanized bees, and mites parasitic on bees, in relation to world beekeeping. See Ref. 143a, pp. 1–12
 43. Crane E, Walker P. 1983. *The Impact of Pest Management of Bees and Pollination*. London: Int. Bee Res. Assoc.
 44. Crepet WL. 1983. The role of insect pollination in the evolution of the angiosperms. In *Pollination Biology*, ed. L Real, pp. 29–50. New York: Academic
 45. Cropper SC, Calder DM. 1990. The floral biology of *Thelymitra epipactoides* (Orchidaceae), and the implications of pollination by deceit on the survival of this rare orchid. *Plant Syst. Evol.* 170:11–27
 46. Cruden RW. 1972. Pollination biology of *Nemophila menziesii* (Hydrophyllaceae) with comments on the evolution of oligolectic bees. *Evolution* 26:373–89
 - 46a. Dafni A, Schmida A. 1996. The possible ecological implications of the invasion of *Bombus terrestris* (L.) (Apidae) at Mt. Carmel, Israel. In *The Conservation of Bees*, ed. A Matheson, SL Buchman, C O'Toole, P Westrich, IH Williams, pp. 183–200. London: Academic
 47. Day MC. 1991. *Towards the Conservation of Aculeate Hymenoptera in Europe*. Strasbourg, France: Counc. Eur.
 48. Delfinado-Baker M. 1988. The tracheal mite of honey bees: a crisis in beekeeping. See Ref. 143a, pp. 493–97
 49. DeMauro MM. 1993. Relationship of breeding system to rarity in the lakeside daisy (*Hymenoxys acaulis* var *glabra*). *Conserv. Biol.* 7:542–50
 50. Didham RK, Ghazoul J, Stork NE, Davis AJ. 1996. Insects in fragmented forests: a functional approach. *Trends Ecol. Evol.* 11:255–60
 51. Donovan BJ. 1990. Selection and importation of new pollinators to New Zealand. *NZ Entomol.* 13:26–32
 52. Dover J, Sotherton N, Gobbett K. 1990. Reduced pesticide inputs on cereal field margins: the effects on butterfly abundance. *Ecol. Entomol.* 15:17–24
 53. Dover JW. 1996. Factors affecting the distribution of satyrid butterflies on arable farmland. *J. Appl. Ecol.* 33:723–34
 54. Dudash MR. 1993. Variation in pollen limitation among individuals of *Sabatia angularis* (Gentianaceae). *Ecology* 74:959–62
 55. Ehrlich PR, Ehrlich AH. 1996. *Betrayal of Science and Reason*. Washington, DC: Island. 335 + xiii pp.
 56. Ehrlich PR, Raven PH. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18:586–608
 57. Eickwort GC. 1988. The origins of mites associated with honeybees. See Ref. 143a, pp. 327–38
 58. Ellstrand NC, Elam DR. 1993. Population genetic consequences of small population size: implications for plant conservation. *Annu. Rev. Ecol. Syst.* 24:217–42
 59. Falk DA. 1992. From conservation biology to conservation practice: strategies for protecting plant diversity. In *Conservation Biology: the Theory and Practice of Nature Conservation, Preservation and Management*, ed. PL Fiedler, SK Jain, pp. 397–431. New York: Chapman & Hall
 60. Falk DA, Millar CJ, Olwell M, eds. 1996. *Restoring Diversity. Strategies for Reintroduction of Endanger. Plants*. Washington, DC: Island. 595 pp.
 61. Feinsinger P. 1983. Coevolution and pollination. In *Coevolution*, ed. DJ Futuyma, M Slatkin, pp. 282–310. Sunderland, MA: Sinauer Assoc.
 62. Feinsinger P. 1987. Approaches to nectarivore-plant interactions in the new world. *Rev. Chil. Hist. Nat.* 60:285–319
 63. Fitts RD, Tepedino VJ, Griswold TL. 1993. The pollination biology of Arizona cliffrose (*Purshia subintegra*), including a report on experimental hybridization with its sympatric congener *P. stansburiana* (Rosaceae). See Ref. 199a, pp. 359–68
 64. Fletcher DJC. 1988. Relevance of the behavioral ecology of African bees to a solution to the Africanized-bee problem. See Ref. 143a, pp. 55–61
 65. Free JB, Butler CG. 1959. *Bumblebees*. New York: Macmillan
 66. Free JB, Ferguson AW. 1980. Foraging of bees on oil-seed rape (*Brassica napus* L.) in relation to the stage of flowering of the crop and pest control. *J. Agric. Sci.* 94:151–54
 67. Fritz AL, Nilsson LA. 1994. How pollinator-mediated mating varies with population size in plants. *Oecologia* 100:451–62

68. Gardner RO, Early JW. 1996. The naturalisation of banyan figs (*Ficus* spp, Moraceae) and their pollinating wasps (Hymenoptera: Agaonidae) in New Zealand. *NZ J. Bot.* 34:103–10
69. Gauld ID, Collins NM, Fitton MG. 1990. *The Biological Significance and Conservation of Hymenoptera in Europe*. Strasbourg, France: Counc. Eur. 47 pp.
70. Gess FW, Gess SK. 1993. Effects of increasing land utilization on species representation and diversity of aculeate wasps and bees in the semi-arid areas of southern Africa. See Ref. 121a, pp. 83–113
71. Grant KA, Grant V. 1967. Effects of hummingbird migration on plant speciation in the California flora. *Evolution* 21:457–65
72. Greathead DJ. 1983. The multi-million dollar weevil that pollinates oil palms. *Antenna* 7:105–7
73. Groom MJ. 1998. Allee effects limit population viability of an annual plant. *Am. Nat.* 151:487–96
74. Hall P, Walker S, Bawa K. 1996. Effect of forest fragmentation on genetic diversity and mating system in a tropical tree, *Pithecellobium elegans*. *Conserv. Biol.* 10:757–68
75. Herrera CM. 1987. Components of pollinator “quality”: comparative analysis of a diverse insect assemblage. *Oikos* 50:79–90
76. Herrera CM. 1988. Variation in mutualisms: the spatio-temporal mosaic of a pollinator assemblage. *Biol. J. Linn. Soc.* 35:95–125
77. Herrera CM. 1989. Pollinator abundance, morphology, and flower visitation rate: analysis of the “quantity” component in a plant-pollinator system. *Oecologia* 80:241–48
78. Herrera CM. 1996. Floral traits and plant adaptation to insect pollinators: a devil’s advocate approach. In *Floral Biology: Studies on Floral Evolution in Animal-Pollinated Plants*, ed. DG Lloyd, SCH Barrett, pp. 65–87. New York: Chapman & Hall
79. Herrera J. 1988. Pollination relationships in southern Spanish Mediterranean shrublands. *J. Ecol.* 76:274–87
80. Heschel MS, Paige KN. 1995. Inbreeding depression, environmental stress, and population size variation in scarlet gilia (*Ipomopsis aggregata*). *Conserv. Biol.* 9:126–33
81. Heywood VH, ed. 1993. *Flowering Plants of the World*. New York: Oxford Univ. Press
82. Howarth FG. 1985. Impacts of alien land arthropods and mollusks on native plants and animals in Hawai’i. In *Hawai’i’s Terrestrial Ecosystems: Preservation and Management*, ed. CP Stone, JM Scott, pp. 149–79. Honolulu: Univ. Hawaii Coop. Natl. Park Resour. Study Unit
83. Howe HF. 1984. Constraints on the evolution of mutualism. *Am. Nat.* 123:764–77
84. Hurlbert AH, Hosoi SA, Temeles EJ, Ewald PW. 1996. Mobility of *Impatiens capensis* flowers: effect on pollen deposition and hummingbird foraging. *Oecologia* 105:243–46
85. Ingram M, Nabhan GP, Buchmann S. 1996. Impending pollination crisis threatens biodiversity and agriculture. *Tropinet* 7:1
86. Ingvarsson PK, Lundberg S. 1995. Pollinator functional response and plant population dynamics: pollinators as a limiting resource. *Evol. Ecol.* 9:421–28
87. Inouye DW. 1983. The ecology of nectar robbing. In *The Biology of Nectaries*, ed. TS Elias, BL Bentley, pp. 153–73. New York: Columbia Univ. Press
88. Inouye DW, Calder WA, Waser NM. 1991. The effect of floral abundance on feeder censuses of hummingbird abundance. *Condor* 93:279–85
89. Janzen DH. 1987. Insect diversity of a Costa Rican dry forest: Why keep it, and how? *Biol. J. Linn. Soc.* 30:343–56
90. Jennersten O. 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. *Conserv. Biol.* 2:359–66
91. Johansen CA. 1977. Pesticides and pollinators. *Annu. Rev. Entomol.* 22:177–92
92. Johnson SD, Bond WJ. 1997. Evidence for widespread pollen limitation of fruiting success in Cape wildflowers. *Oecologia* 109:530–34
93. Jordano P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *Am. Nat.* 129:657–77
94. Kearns CA. 1992. Anthophilous fly distribution across an elevation gradient. *Am. Midl. Nat.* 127:172–82
95. Kearns CA, Inouye DW. 1994. Fly pollination of *Linum lewisii* (Linaceae). *Am. J. Bot.* 81:1091–95
96. Kearns CA, Inouye DW. 1997. Pollinators, flowering plants, and conservation biology. *BioScience* 47:297–307

97. Kesseli RV. 1992. Population biology and conservation of rare plants. In *Applied Population Biology*, ed. SK Jain, LW Botsford, pp. 69–90. Dordrecht, The Netherlands: Kluwer Acad.
98. Kevan PG. 1974. Pollination, pesticides and environmental quality. *BioScience* 24:198–99
99. Kevan PG. 1975. Forest application of the insecticide Fenitrothion and its effect on wild bee pollinators (Hymenoptera: Apoidea) of lowbush blueberries (*Vaccinium* spp.) in southern New Brunswick, Canada. *Biol. Conserv.* 7:301–9
100. Kevan PG. 1975. Pollination and environmental conservation. *Environ. Conserv.* 2:293–98
101. Kevan PG. 1986. Pollinating and flower visiting insects and the management of beneficial and harmful insects and plants. In *Biological Control in the Tropics: Proc. First Reg. Symp. Biol. Control, Univ. Pertanian Malaysia, Serdang, 4–6 Sept., 1985*, ed. MY Hussein, AG Ibrahim, pp. 439–52. Serdang, Selangor, Malaysia: Penerbit Univ. Pertanian
102. Kevan PG. 1991. Pollination: keystone process in sustainable global productivity. *Acta Hort.* 288:103–9
103. Kevan PG. 1998. Pollinators in agroecosystems: their keystone role in sustainable productivity and biodindication. In *Biodiversity in Agroecosystems Role of Sustainability and Biodindication*, ed. M Paoletti. New York: Elsevier. In press
104. Kevan PG, Clark EA, Thomas FG. 1990. Pollination: a crucial ecological and mutualistic link in agroforestry and sustainable agriculture. *Proc. Entomol. Soc. Ontario* 121:43–48
105. Kevan PG, Lavery TM. 1990. A brief survey and caution about importing alternative pollinators into Canada. *Can. Beekeep.* 15:176–77
106. Kevan PG, Plowright RC. 1989. Fenitrothion and insect pollination. In *Environmental Effects of Fenitrothion Use in Forestry: Impacts on Insect Pollinators, Songbirds, and Aquatic Organisms*, ed. WR Ernst, PA Pearce, TL Pollock, pp. 13–42. Dartmouth, Nova Scotia: Environ. Canada
107. Klemm M. 1996. Man-made bee habitats in the anthropogenous landscape of central Europe—substitutes for threatened or destroyed riverine habitats? See Ref. 130a, pp. 17–34
108. Klinkhamer PGL, de Jong TJ, de Bruyn G-J. 1989. Plant size and pollinator visitation in *Cynoglossum officinale*. *Oikos* 54:201–4
109. Knowles D. 1983/4. Flying jewels. *Geo* 5:46–57
110. Krannitz PG, Maun MA. 1991. An experimental study of floral display size and reproductive success in *Viburnum opulus*: importance of grouping. *Can. J. Bot.* 69:394–99
111. Kratochwil A. 1988. Co-phenology of plants and anthophilous insects: a historical area-geographical interpretation. *Entomol. Gen.* 13:67–80
112. Kunin WE. 1992. Density and reproductive success in wild populations of *Diplotaxis erucoides* (Brassicaceae). *Oecologia* 91:129–33
113. Kunin WE. 1993. Sex and the single mustard: population density and pollinator behavior effects on seed-set. *Ecology* 74:2145–60
114. Kunin WE. 1997. Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. *J. Ecol.* 85:225–34
115. Kwak MM. 1987. Pollination and pollen flow disturbed by honeybees in bumblebee-pollinated *Rhinanthus* populations? In *Disturbance in Grasslands*, ed. J van Andel, JP Bakker, RW Snaydon, pp. 273–83. Dordrecht, The Netherlands: Dr. W. Junk
116. Kwak MM. 1995. Pollination ecology and endangered plant species. In *Proc. Second CONNECT Workshop on Landscape Ecol.*, ed. F Skov, J Komdeur, G Fry, J Knudsen, pp. 54–57. Kalo, Denmark: Environ. Res. Inst.
117. Kwak MM. 1996. Bumble bees at home and at school. In *Bumble Bees for Pleasure and Profit*, ed. A Matheson, pp. 12–23. Cardiff, UK: Int. Bee Res. Assoc.
118. Kwak MM, Kremer P, Boerrichter E, van den Brand C. 1991. Pollination of the rare species *Phyteuma nigrum* (Campanulaceae): flight distances of bumblebees. *Proc. Exp. Appl. Entomol.* 2:131–36
119. Lagerlöf J, Stark J, Svensson B. 1992. Margins of agricultural fields as habitats for pollinating insects. *Agric. Ecosyst. Environ.* 40:117–24
120. Lammers TG, Weller SG, Sakai AK. 1987. Japanese White-eye, an introduced passerine, visits the flowers of *Clermontia arborescens*, an endemic Hawaiian Lobelioid. *Pac. Sci.* 41:74–77
121. Lamont BB, Klinkhamer PGL, Witkowski ETF. 1993. Population fragmentation may reduce fertility to zero in

- Banksia goodii*—a demonstration of the Allee effect. *Oecologia* 94:446–50
- 121a. LaSalle J, Gauld ID, ed. 1993. *Hymenoptera and Biodiversity*. Wallingford, UK: CAB Int.
 122. Les DH, Reinhartz JA, Esselman EJ. 1991. Genetic consequences of rarity in *Aster furcatus* (Asteraceae), a threatened, self-incompatible plant. *Evolution* 45:1641–50
 123. Lesica P. 1993. Loss of fitness resulting from pollinator exclusion in *Silene spaldingii* (Caryophyllaceae). *Madroño* 40:193–201
 124. Light N. 1994. Abuzz about bumblebees. *Am. Fruit Grow.* 114:20–21
 125. Lord JM. 1991. Pollination and seed dispersal in *Freyinetia baueriana*, a dioecious liane that has lost its bat pollinator. *NZ J. Bot.* 29:83–86
 126. Louda SM, Potvin MA. 1995. Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. *Ecology* 76:229–45
 127. Lubbers AE, Lechowicz MJ. 1989. Effects of leaf removal on reproduction vs. belowground storage in *Trillium grandiflorum*. *Ecology* 70:85–96
 128. Mal TK, Lovett-Doust J, Lovett-Doust L, Mulligan GA. 1992. The biology of Canadian weeds. 100. *Lythrum salicaria*. *Can. J. Plant Sci.* 72:1305–30
 129. Maron JL, Simms EL. 1997. Effect of seed predation on seed bank size and seedling recruitment of bush lupine (*Lupinus arboreus*). *Oecologia* 111:76–83
 130. Martinez ND. 1992. Constant connectance in community food webs. *Am. Nat.* 139:1208–18
 - 130a. Matheson A, Buchmann SL, O'Toole C, Westrich P, Williams IH, ed. 1996. *The Conservation of Bees*. New York: Academic
 131. Maunder M. 1992. Plant reintroduction—an overview. *Biodivers. Conserv.* 1:51–61
 132. McKey D. 1989. Population biology of figs: applications for conservation. *Experientia* 45:661–73
 133. Menges ES. 1995. Factors limiting fecundity and germination in small populations of *Silene regia* (Caryophyllaceae), a rare hummingbird-pollinated prairie forb. *Am. Midl. Nat.* 133:242–55
 134. Moldenke AR, Lincoln PG. 1979. Pollination ecology in montane Colorado: a community analysis. *Phytologia* 42:349–79
 135. Montalvo AM, Ackerman JD. 1987. Limitation to fruit production in *Ionopsis utricularioides* (Orchidaceae). *Biotropica* 19:24–31
 136. Morse RA. 1988. Preface. See Ref. 143a, pp. xvii
 137. Morse RA. 1991. Honeybees forever. *Trends Ecol. Evol.* 6:337–38
 138. Murcia C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends Ecol. Evol.* 10:58–62
 139. Murcia C. 1996. Forest fragmentation and the pollination of neotropical plants. In *Forest Patches in Tropical Landscapes*, ed. J Schelhas, R Greenberg, pp. 19–36. Washington, DC: Island
 140. Nabhan GP. 1996. *Pollinator Redbook*. Vol. 1: *Global List of Threatened Vertebrate Wildlife Species Serving as Pollinators for Crops and Wild Plants*. Tucson, AZ: Arizona-Sonora Desert Mus. & Forgot. Pollinat. Camp. Monogr.
 141. Nabhan GP, Buchmann SL. 1997. Services provided by pollinators. In *Nature's Services. Societal Dependence on Natural Ecosystems*, ed. GC Daily, pp. 133–50. Washington, DC: Island
 142. Natl. Res. Council. Can. 1981. *Pesticide-Pollinator Interactions*. NRC Assoc. Comm. Sci. Criteria Environ. Qual. Publ. NRCC No. 18471. Ottawa, Canada: Natl. Res. Council. Can. Environ. Secr.
 143. Nat. Conserv. Council. 1991. *A Review of the Scarce and Threatened Bees, Wasps and Ants of Great Britain*. Peterborough, UK: Nat. Conserv. Council.
 - 143a. Needham GR, Page RE Jr, Delfinado-Baker M, Bowman CE, eds. 1988. *Africanized Honey Bees and Bee Mites*. New York: Wiley
 144. Olesen JM, Jain SK. 1994. Fragmented plant populations and their lost interactions. In *Conservation Genetics*, ed. V Loeschcke, J Tomiuk, SK Jain, pp. 417–26. Basel: Birkhäuser
 145. Osborne JL, Corbet SA. 1994. Managing habitats for pollinators in farmland. *Aspects Appl. Biol.* 40:207–15
 146. Osborne JL, Williams IH, Corbet SA. 1991. Bees, pollination and habitat change in the European Community. *Bee World* 72:99–116
 147. O'Toole C. 1993. Diversity of native bees and agroecosystems. See Ref. 121a, pp. 169–96
 148. Parker FD, Batra SWT, Tepedino VJ. 1987. New pollinators for our crops. *Agric. Zool. Rev.* 2:279–304
 149. Paton DC. 1985. Food supply, population structure, and behaviour of New Holland Honeyeaters *Phylidonyris novaehollandiae* in woodlands near

- Horsham, Victoria. In *Birds of Eucalypt Forests and Woodlands: Ecology, Conservation, and Management*, ed. A Keast, HF Recher, H Ford, D Saunders, pp. 222–30. Sydney, Aust.: R. Aust. Ornithol. Union and Surry & Beatty
150. Paton DC. 1993. Honeybees in the Australian environment. *BioScience* 43:95–103
151. Paton DC. 1996. *Overview of Feral and Managed Honeybees in Australia: Distribution, Abundance, Extent of Interactions with Native Biota, Evidence of Impacts and Future Research*. Canberra, Aust.: Aust. Nat. Conserv. 71 pp.
152. Pavlik BM, Ferguson N, Nelson M. 1993. Assessing limitations on the growth of endangered plant populations: 2. Seed production and seed bank dynamics of *Erysimum capitatum* ssp. *angustatum* and *Oenothera deltoidea* ssp. *howellii*. *Biol. Conserv.* 65:267–78
153. Peach ML, Alston DG, Tepedino VJ. 1994. Bees and bran bait: Is carbaryl bran bait lethal to alfalfa leafcutting bee (Hymenoptera: Megachilidae) adults or larvae? *J. Econ. Entomol.* 87:311–17
154. Peach ML, Tepedino VJ, Alston DG, Griswold TL. 1993. Insecticide treatments for rangeland grasshoppers: potential effects on the reproduction of *Pediocactus sileri* (Englem.) Benson (Cactaceae). See Ref. 199a, pp. 309–19
155. Percy DM, Cronk QCB. 1997. Conservation in relation to mating system in *Nesohedytis arborea* (Rubiaceae), a rare endemic tree from St Helena. *Biol. Conserv.* 80:135–45
156. Petanidou T, den Nijs HCM, Ellis-Adam AC. 1991. Comparative pollination ecology of two rare Dutch *Gentiana* species, in relation to population size. *Acta Hort.* 288:308–12
157. Petanidou T, Ellis WE. 1993. Pollinating fauna of a phryganic ecosystem: composition and diversity. *Biodivers. Lett.* 1:9–22
158. Petit S, Pors L. 1996. Survey of columnar cacti and carrying capacity for nectar-feeding bats on Curaçao. *Conserv. Biol.* 10:769–75
159. Pimentel D, Wilson C, McCullum C, Huang R, Dwen P, et al. 1997. Economic and environmental benefits of biodiversity. *BioScience* 47:747–57
160. Pimm SL. 1991. *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities*. Chicago: Univ. Chicago Press
161. Plowright RC, Rodd FH. 1980. The effect of aerial spraying on hymenopterous pollinators in New Brunswick. *Can. Entomol.* 112:259–69
162. Polis GA. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *Am. Nat.* 138:123–55
163. Pomeroy N. 1997. *Message from BOMBUS-L listserv list, 27 March.*
164. Powell AH, Powell GVN. 1987. Population dynamics of male euglossine bees in Amazonian forest fragments. *Biotropica* 19:176–79
165. Prescott-Allen C, Prescott-Allen R. 1986. *The First Resource: Wild Species in the North American Economy*. New Haven, CT: Yale Univ. Press
166. Price MV, Waser NM. 1998. Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology*. 79:1261–71
167. Proctor M, Yeo P, Lack A. 1996. *The Natural History of Pollination*. Portland, OR: Timber
168. Pyle RM. 1997. Burning bridges. *Wings* 21:22–23
169. Rathcke BJ, Jules ES. 1993. Habitat fragmentation and plant-pollinator interactions. *Curr. Sci.* 65:273–77
170. Raven PH. 1987. The scope of the plant conservation problem world-wide. In *Botanic Gardens and the World Conservation Strategy*, ed. D Bramwell, O Harman, V Heywood, H Syngé, pp. 19–20. London: Academic
171. Richards KW. 1984. *Alfalfa Leaf-cutter Bee Management in Western Canada. Publication 1495/E*. Ottawa, Can.: Agric. Can.
172. Richards KW. 1993. Non-*Apis* bees as crop pollinators. *Rev. Suisse Zool.* 100:807–22
173. Rinderer TE. 1988. Evolutionary aspects of the Africanization of honey-bee populations in the Americas. See Ref. 143a, pp. 13–28
174. Ritter W. 1988. *Varroa jacobsoni* in Europe, the tropics, and subtropics. See Ref. 143a, pp. 349–69
175. Roll J, Mitchell RJ, Cabin RJ, Marshall DL. 1997. Reproductive success increases with local density of conspecifics in the desert mustard *Lesquerella fendleri*. *Conserv. Biol.* 11:738–46
176. Roubik DW. 1978. Competitive interactions between neotropical pollinators and Africanized honey bees. *Science* 201:1030–32
177. Roubik DW. 1980. Foraging behavior of competing Africanized honeybees and stingless bees. *Ecology* 61:836–45

178. Roubik DW. 1983. Experimental community studies: time-series tests of competition between African and neotropical bees. *Ecology* 64:971–78
179. Roubik DW. 1989. *Ecology and Natural History of Tropical Bees*. Cambridge, UK: Cambridge Univ. Press
180. Roubik DW. 1991. Aspects of Africanized honey bee ecology in tropical America. In *The "African" Honey Bee*, ed. M Spivak, DJC Fletcher, MD Breed, pp. 259–81. Boulder, CO: Westview
181. Roubik DW. 1992. Loose niches in tropical communities: Why are there so few bees and so many trees? In *Effects of Resource Distribution on Animal-Plant Interactions*, ed. MD Hunter, T Ohgushi, P Price, pp. 327–54. New York: Academic
182. Roubik DW. 1993. Tropical pollinators in the canopy and understory: field data and theory for stratum preferences. *J. Insect Behav.* 6:659–73
183. Roubik DW. 1996. African honey bees as exotic pollinators in French Guiana. See Ref. 130a, pp. 173–82
184. Roubik DW. 1996. Measuring the meaning of honey bees. See Ref. 130a, pp. 163–72
185. Roubik DW, Moreno JE, Vergara C, Wittmann D. 1986. Sporadic food competition with the African honey bee: projected impact on neotropical social bees. *J. Trop. Ecol.* 2:97–111
186. Sampson AW. 1952. *Range Management, Principles and Practices*. New York: Wiley
187. Samways MJ. 1994. *Insect Conservation Biology*. London: Chapman & Hall
188. Sanford MT. 1996. A pollination crisis? *APIS Apic. Issues Answ. Fla. Coop. Ext. Newsl.* 14:1
189. Saure C. 1996. Urban habitats for bees: the example of the city of Berlin. See Ref. 130a, pp. 47–53
190. Schaffer WM, Zeh DW, Buchmann SL, Kleinhaus S, Schaffer MV, Antrim J. 1983. Competition for nectar between introduced honey bees and native North American bees and ants. *Ecology* 64:564–77
191. Schemske DW, Husband BC, Ruckelshaus MH, Goodwillie C, Parker IM, Bishop JG. 1994. Evaluating approaches to the conservation of rare and endangered plants. *Ecology* 75:584–606
192. Schmitt J. 1983. Flowering plant density and pollinator visitation in *Senecio*. *Oecologia* 60:97–102
193. Scott-Dupree CD, Winston ML. 1987. Wild bee pollinator diversity and abundance in orchard and uncultivated habitats in the Okanagan Valley, British Columbia. *Can. Entomol.* 119:735–45
194. Senft D. 1990. Protecting endangered plants. *Agric. Res.* 38:16–18
195. Sih A, Baltus M. 1987. Patch size, pollinator behavior, and pollinator limitation in catnip. *Ecology* 68:1679–90
196. Simmons CH Jr, ed. 1996. *Plymouth Colony Records. Wills and Inventories, 1633–1669*. Camden, ME: Picton
197. Sipes SD, Tepedino VJ. 1995. Reproductive biology of the rare orchid, *Spiranthes diluvialis*: breeding system, pollination, and implications for conservation. *Conserv. Biol.* 9:929–38
198. Sipes SD, Tepedino VJ. 1996. Pollinator lost? Reproduction by the enigmatic Jones Cycladenia, *Cycladenia humilis* var. *jonesii* (Apocynaceae). In *Southwestern Rare and Endanger. Plants: Proc. 2nd Conf., 1995 Sept. 11–14. Flagstaff, AZ. General Technical Report RM-GTR-283*, ed. J Maschinski, HD Hammond, L Holter, pp. 158–66. Fort Collins, CO: USDA For. Serv. Rocky Mt. For. Range Exp. Stn.
199. Sipes SD, Tepedino VJ, Bowlin WR. 1993. The pollination and reproductive ecology of *Spiranthes diluvialis* Sheviak (Orchidaceae). See Ref. 199a, pp. 320–33
- 199a. Sivinski R, Lightfoot K, eds. 1993. *Proc. Southwest. Rare and Endanger. Plant Conf.* Santa Fe, NM: NM For. Resour. Conserv. Div.
200. Smith TB, Freed LA, Lepson JK, Crothers JH. 1995. Evolutionary consequences of extinctions in populations of a Hawaiian honeycreeper. *Conserv. Biol.* 9:107–13
201. Southwick EE, Southwick L Jr. 1992. Estimating the economic value of honey bees (Hymenoptera: Apidae) as agricultural pollinators in the United States. *J. Econ. Entomol.* 85:621–33
202. Sowig P. 1989. Effects of flowering plant's patch size on species composition of pollinator communities, foraging strategies, and resource partitioning in bumblebees (Hymenoptera: Apidae). *Oecologia* 78:550–58
203. Spears EE Jr. 1987. Island and mainland pollination ecology of *Centrosoma virginianum* and *Opuntia stricta*. *J. Ecol.* 75:351–62
204. Steiner KE. 1993. Has *Ixianthes* (Scrophulariaceae) lost its special bee? *Plant Syst. Evol.* 185:7–16
205. Steiner KE, Whitehead VB. 1996. The consequences of specialization for pollination in a rare South African shrub,

- Ixianthes retzioides* (Scrophulariaceae). *Plant Syst. Evol.* 201:131–38
206. Stephen WP, Bohart GE, Torchio PF. 1969. *The Biology and External Morphology of Bees, with a Synopsis of the Genera of Northwestern America*. Corvallis, OR: Oreg. State Univ. Agric. Exp. Stn.
207. Stephenson AG. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annu. Rev. Ecol. Syst.* 12:253–79
208. Stolzenburg W. 1993. Lucky clovers. *Nat. Conserv.* 43:6
209. Stouffer PC, Bierregaard RO Jr. 1995. Effects of forest fragmentation on understory hummingbirds in Amazonian Brazil. *Conserv. Biol.* 9:1085–94
210. Struck M. 1994. Flowers and their insect visitors in the arid winter rainfall region of southern Africa: observations on permanent plots. Composition of the anthophilous insect fauna. *J. Arid. Env.* 28:45–50
211. Sugden EA. 1985. Pollinators of *Astragalus monoensis* Barneby (Fabaceae): new host records; potential impact of sheep grazing. *Gt. Basin Natur.* 45:299–312
212. Sugden EA, Pyke GH. 1991. Effects of honey bees on colonies of *Exoneura asimillimia*, an Australian native bee. *Aust. J. Ecol.* 16:171–81
213. Sugden EA, Thorp RW, Buchmann SL. 1996. Honey bee-native bee competition: focal point for environmental change and apicultural response in Australia. *Bee World* 77:26–44
214. Taylor OR. 1988. Ecology and economic impact of African and Africanized honey bees. See Ref. 143a, pp. 29–44
215. Tepedino VJ. 1979. The importance of bees and other insect pollinators in maintaining floral species composition. *Gt. Basin Nat. Mem.* 3:139–50
216. Tepedino VJ, Sipes SD, Barnes JL, Hickerson LL. 1997. The need for “extended care” in conservation: examples from studies of rare plants in the western United States. *Acta Hortic.* 437:245–48
217. Tepedino VJ, Stanton NL. 1980. Spatiotemporal variation in phenology and abundance of floral resources on short-grass prairie. *Gt. Basin Natur.* 40:197–215
218. Thaler GR, Plowright RC. 1980. The effect of aerial insecticide spraying for spruce budworm control on the fecundity of entomophilous plants in New Brunswick. *Can. J. Bot.* 58:2022–27
219. Thomson JD. 1981. Spatial and temporal components of resource assessment by flower-feeding insects. *J. Anim. Ecol.* 50:49–59
220. Thomson JD. 1993. The queen of forage and the bumblebee revolution: a conference with an attitude. *Trends Ecol. Evol.* 8:41–42
221. Thomson JD, Plowright RC, Thaler GR. 1985. Matabic insecticide spraying, pollinator mortality, and plant fecundity in New Brunswick forests. *Can. J. Bot.* 63:2056–61
222. Thomson JN, Pellmyr O. 1992. Mutualism with pollinating seed parasites amid co-pollinators: constraints on specialization. *Ecology* 73:1780–91
223. Thorp RW. 1996. Resource overlap among native and introduced bees in California. See Ref. 130a, pp. 143–51
224. Torchio PF. 1990. Diversification of pollination strategies for U.S. crops. *Environ. Entomol.* 19:1649–56
225. Torchio PF. 1991. Bees as crop pollinators and the role of solitary species in changing environments. *Acta Hortic.* 288:49–61
226. Totland O. 1993. Pollination in alpine Norway: flowering phenology, insect visitors, and visitation rates in two plant communities. *Can. J. Bot.* 71:1072–79
227. van Treuren R, Bijlsma R, Ouborg NJ, Van Delden W. 1993. The effects of population size and plant density on outcrossing rates in locally endangered *Salvia pratensis*. *Evolution* 47:1094–104
228. van Treuren R, Bijlsma R, Van Delden W, Ouborg NJ. 1991. The significance of genetic erosion in the process of extinction. I. Genetic differentiation in *Salvia pratensis* and *Scabiosa columbaria* in relation to population size. *Heredity* 66:181–89
229. Vinson SB, Frankie GW, Barthell J. 1993. Threats to the diversity of solitary bees in a neotropical dry forest in Central America. See Ref. 121a, pp. 53–82
230. Waring GH, Loope LL, Medeiros AC. 1993. Study on the use of alien versus native plants by nectarivorous forest birds on Maui, Hawaii. *Auk* 110:917–20
231. Waser NM. 1979. Pollinator availability as a determinant of flowering time in ocotillo (*Fouquieria splendens*). *Oecologia* 39:107–21
232. Waser NM, Chittka L, Price MV, Williams N, Ollerton J. 1996. Generalization in pollination systems, and why it matters. *Ecology* 77:279–96
233. Waser NM, Price MV. 1983. Optimal and actual outcrossing in plants, and the

- nature of plant-pollinator interaction. In *Handbook of Experimental Pollination Biology*, ed. CE Jones, RJ Little, pp. 341–59. New York: Van Nostrand Reinhold
234. Washitani I. 1996. Predicted genetic consequences of strong fertility selection due to pollinator loss in an isolated population of *Primula sieboldii*. *Conserv. Biol.* 10:59–64
 235. Watanabe ME. 1994. Pollination worries rise as honey bees decline. *Science* 265:1170
 236. Watkins M. 1997. Resistance and its relevance to beekeeping. *Bee World* 78:15–22
 237. Wcislo WT, Cane JH. 1996. Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies. *Annu. Rev. Entomol.* 41:257–86
 238. Wenner AM. 1993. The honey bees of Santa Cruz. *Bee Cult.* 121:272–75
 239. Westerkamp C. 1996. Pollen in bee-flower relations: some considerations on melittophily. *Bot. Acta* 109:325–32
 240. Westerkamp C. 1997. Keel blossoms: bee flowers with adaptations against bees. *Flora* 192:125–32
 241. Westrich P. 1996. Habitat requirements of central European bees and the problems of partial habitats. See Ref. 130a, pp. 1–16
 242. Westrich P, Schwenninger HR. 1997. Habitatwahl, Blütennutzung und Bestandsentwicklung der Zweizelligen Sandbiene (*Andrena lagopus* Latr.) in Südwest-Deutschland (Hymenoptera, Apidae). *Z. Ökol. Nat.schutz* 6:33–42
 243. Williams CS. 1995. Conserving Europe's bees: why all the buzz. *Trends Ecol. Evol.* 10:309–10
 244. Williams IH. 1996. Aspects of bee diversity and crop pollination in the European Union. See Ref. 130a, pp. 63–80
 245. Williams IH, Simpkins JR, Martin AP. 1991. Effect of insect pollination on seed production in linseed (*Linum usitatissimum*). *J. Agric. Sci.* 117:75–79
 246. Williams PH. 1986. Environmental change and the distributions of British bumble bees (*Bombus* Latr.). *Bee World* 67:50–61
 247. Wolf M, Shmida A. 1995. Association of flower and pollinator activity in the Negev Desert, Israel. *Adv. Geoeol.* 28:173–92