

Best Wishes,
Carol

Pollinators, Flowering Plants, and Conservation Biology

Much remains to be learned about pollinators and plants

Carol Ann Kearns and David William Inouye

More than a century ago, Darwin (1859) observed that “the number of bumblebees in any district depends in a great measure upon the number of field-mice, which destroy their combs and nests...the number of mice is largely dependent, as everyone knows, on the number of cats...it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district!” (p. 125). Darwin recognized the importance of interactions among organisms, specifically the role that pollinators play as links in communities. Yet, almost 140 years later, our understanding of pollination interactions is still rudimentary. The extent of dependence and linkage in pollination sys-

Carol Ann Kearns is an instructor in Environmental, Population, and Organismic Biology and assistant director of the Williams Village Residential Academic Program in environmental science, Campus Box 334, University of Colorado, Boulder, CO 80309. Her interests are in pollination of montane and alpine plants, plant population genetics, and conservation biology. David William Inouye is an associate professor at the University of Maryland in both the Zoology and Plant Biology departments, College Park, MD 20742. He also directs the graduate program in Sustainable Development and Conservation Biology at the University of Maryland and conducts long-term studies of plants and insects at the Rocky Mountain Biological Laboratory, Crested Butte, CO 81224. © 1997 American Institute of Biological Sciences.

The ultimate fate of many plants may depend on preserving their mutualistic relationships with pollinators and with the web of organisms that affect both plant and pollinator

tems is currently under scrutiny as an issue affecting conservation of biodiversity (Figure 1).

Plant-pollinator mutualisms date back to the Cretaceous period, when insects began to acquire food from flowers, and flowers achieved higher reproductive success through the movement of pollen by insects. Today, at least 67% of flowering plants depend on insects for pollination (Tepedino 1979), and others depend on birds and mammals. For these plants to persist, pollinators are as critical as light and water (Levin 1971). However, comparatively little is known about pollinators. In addition, the pollination requirement of most wild species remains unknown: For example, the pollinators of 14 of 16 endangered plant species near the United States-Mexico border have not been determined (Nabhan 1996), and little or nothing is known about the pollination requirements of approximately one-third of the Euro-

pean Union's crop plants (Williams 1995).

In this article, we review variation in dependence by plants on pollinators, the potential for a cascade of effects in a community resulting from loss of a plant-pollinator mutualism, current threats to plants and pollinators, and possible management issues. Much of our discussion will focus on bees, because bee life histories are intimately linked with those of flowering plants. Bees are active, constant foragers, and they are reliable pollinators because they must continually forage for their own nutritional needs and those of their progeny. Approximately 30% of human food is derived from bee-pollinated crops (O'Toole 1993), and thousands of wild plants depend on the services of bees for seed and fruit formation. Thus, reductions in bee abundance could have serious implications for both natural and agricultural ecosystems.

Although bees are major pollinators, it is estimated that less than two-thirds of the world's bee species have been named and described (Buchman and Nabhan 1996). Even in well-studied areas, such as western Europe, estimates of the number of bee species vary from 2000 to 4500 (Williams 1995). Nevertheless, large declines of certain types of bees have been documented in Germany, Austria, Britain, the former Soviet Union, Poland, Italy, and Canada (O'Toole 1993), and in Costa Rica (Janzen 1974, Vinson et al. 1993). In North America, where farmers tend to be heavily depen-

Figure 1. A muscoid fly pollinator (*Thricops* spp.) collects nectar and pollen from a *Potentilla gracilis* flower in montane Colorado. Flies are an example of a little-known category of flower visitors that are probably important in all major ecosystems, from tropical to alpine.



dent on introduced domesticated honeybees for crop pollination, honeybee numbers have declined by approximately 25% since 1990 (Nabhan 1996). In addition to declining bee numbers, other disruptions of natural pollination systems have been documented in many different parts of the world (Aizen and Feinsinger 1994a, Buchmann and Nabhan 1996, Cox 1983, Cropper and Calder 1990, Gess and Gess 1993, Ginsburg 1983, Paton 1993, Roubik et al. 1986, Schaffer et al. 1979, Sugden and Pyke 1991).

Pollinator loss can affect plants in several ways (Tepedino 1979). Loss of, or reduced, seed set is the most obvious result. In addition, a scarcity of pollinators may affect a plant's mating system, resulting in the production of less vigorous offspring. This is because, in the absence of pollinators, a higher percentage of seeds may be set through self-pollination, decreasing heterozygosity and increasing the expression of deleterious traits associated with inbreeding. Smaller pollen loads can also reduce the opportunity for pollen competition; different rates of pollen tube growth through the style can result in competition, with the more vigorous pollen grains fertilizing the ovules. In some species, there is a demonstrable correlation between the rate of pollen tube growth and vigor of the resulting progeny (Snow and Spira 1991); thus, reduced pollen loads—and a consequent reduction in pollen competition—could potentially decrease fitness. On a broader scale, loss of

pollinators or disruption of pollination systems may cause reduced seed and fruit production and, ultimately, plant extinction. Any of these events will affect the organisms that consume seeds, fruits, or plants or that use plants for nest construction.

Although the loss of individual species is of great public concern, the extinction of an ecological process may go unnoticed for some time because it is a more subtle loss whose effects are difficult to predict. The ultimate fate of many plants may depend on preserving their mutualistic relationships with pollinators and with the web of organisms that affect both plant and pollinator.

Threats to pollinators

A number of threats to pollinators have been identified. These include habitat alteration, introductions of alien pollinators, and pesticide poisoning (Bond 1994).

Habitat alteration. Agriculture, grazing, fragmentation of native landscapes, and development of areas that once supported wild vegetation all cause the loss of native food plants, rendezvous plants, and nesting sites used by pollinators. Pollinators may depend on native plants because they are not always able to access food rewards from introduced flowers (O'Toole 1993). Many bees not only require large numbers of

flowers to provide nectar and pollen, but also need a variety of flowering plants to sustain them throughout the growing season. Oligolectic insects, such as some bees and some butterfly larvae, depend on specific plants for survival and persistence of their populations.

In addition to food requirements, pollinating organisms often have specific nesting requirements. Some bee species nest in cavities in the ground, such as old rodent burrows, spaces under rocks, or holes excavated in sand or soft dirt. Many other types of bees nest in hollow twigs. As land is developed for human activity, the availability of twigs, rodent burrows, and suitable nesting substrates typically decreases.

Agriculture. In agricultural areas, large-scale monoculture of crops reduces the amount of land available to support wild vegetation. With the increasing mechanization of agriculture, the number and area of hedgerows and uncultivated patches decrease, reducing the number of native plants available as pollen and nectar sources (O'Toole 1993, Williams 1986). For example, in Great Britain, areas of low bumblebee density correspond to areas of intensive agriculture. In such areas, land previously considered of marginal value has been "improved" by draining grasslands and removing hedgerows; these changes have resulted in decreased habitat diversity (Williams 1986). Comparable effects have been reported for Germany (Williams 1986). In Poland, the number of bumblebees on crops is correlated with the crop field's proximity to forests, meadows, and pastures (Williams 1986). Similarly, in Canada, native pollinators have declined as alfalfa fields cover more and more prairies. In addition, in parts of Europe, the use of insecticides on agricultural lands has been blamed for decreasing bee abundance (Williams 1986).

Grazing. From their work in South Africa, Gess and Gess (1993) determined that grazing livestock alters habitat sufficiently to affect pollinators. They documented changes in availability of nesting sites, water resources, and vegetation that could have direct negative effects on species diversity and population sizes of

bees and wasps. Trampling of vegetation by livestock can directly destroy the nests of ground-nesting species and can compact the soil, constraining nest formation. In addition, the people who tend livestock in these areas of South Africa collect wood for fuel, thus reducing the availability of hollow twigs that provide nesting sites for some bee species.

Grazing also affects bees by decreasing water availability. Both ground-nesting and cavity-nesting bees must collect water for use in nest construction. Most bees cannot obtain water from livestock water tanks with steep sides, or even ponds without sloping edges, but need to stand at the edge of shallow water. Tampering with the natural water supply to provision cattle or produce crops often modifies water availability for bees.

In some areas, selective grazing by livestock has decreased the number of plant species (Gess and Gess 1983). One species, *Galenia africana* (Aizoaceae), which tends to become dominant, is not attractive to pollinators or livestock. As native plant species that were used originally as pollen and nectar sources disappear, the total number of bees that can be supported in the area decreases, in turn potentially decreasing seed set and further reducing diversity.

Dramatic reductions in bee numbers and species diversity have been documented in areas of the Guanacaste Province of Costa Rica that were deforested to support cattle (Janzen 1974, Vinson et al. 1993). The number of oil-collecting bees is decreasing as the forest is destroyed (Vinson et al. 1993). Many of the large, solitary *Centris* bees (Centridini; Anthophoridae) in the dry forest of Costa Rica need dead wood for nests. Female bees provision their nests with the pollen of several tree species and with oil collected largely from *Byrsonima crassifolia* trees (Malphiaceae). Oil collectors are major pollinators of *B. crassifolia* (Vinson et al. 1993). Male and female *Centris* bees are generally pollinators of different plant species, and thus many species are linked by pollination associations.

African pasture grass (*Hyparrhenia rufa*) has been introduced to defor-

ested areas of Guanacaste Province because it grows well and provides good fodder for beef cattle. Each year, ranchers set fire to the grass fields to clear them of trees and shrubs. The taller African pasture grass supports a hotter fire than the native grasses, and the fires often spread to forested reserves. These intense fires are strong enough to burn through the bark of most oil-producing plant species, and those trees that do manage to survive fires have reduced oil production. Moreover, fire allows grasses to invade farther into the forest each year. The loss of dead wood results in the loss of nesting sites for bees, and the loss of oil plants results in decreased provisions for bee development. Furthermore, as the forest becomes less dense, ground temperatures increase, becoming too high for bees to develop normally in any nests that remain.

Habitat fragmentation. Development can fragment natural habitats, isolating remnants of plant populations. Endangered plants often exist in "ecological traps" (Stebbins 1979) surrounded by different habitats. They may lack the genetic diversity that would allow them to colonize these different habitats. Small populations can also suffer from reduced pollen delivery or reduced quality of the pollen delivered. For example, Lamont et al. (1993) found that population fragmentation reduced fertility to zero in *Banksia goodii* (Proteaceae). This species is a highly outcrossing species pollinated by birds (honeyeaters) and mammals (honey possums). Flowers in small populations either receive fewer visits from pollinators or receive pollen from sibling plants, which results in low seed production. Furthermore, small populations are sometimes bypassed by pollinators because some types of pollinators exhibit density-dependent foraging behavior, preferring large floral displays to isolated flowers (the Allee effect; Lamont et al. 1993).

Like plants, pollinators may persist in ecological traps as a result of habitat fragmentation caused by development and the associated loss of nest sites and food plants. Research conducted by Jennersten (1988) in Sweden illustrates that fragmented regions may harbor fewer

pollinators, and the plants that remain may thus suffer reduced reproductive success. Jennersten (1988) found that self-compatible *Dianthus deltoides* (Caryophyllaceae) produced more seed in areas of continuous meadow and forest than in patchy fragments separated by cultivated fields of barley and oats. Moreover, the crop fields, and the limited wild spaces between them, contained few nectar plants to provision pollinators, whereas the continuous fields and forest had a greater diversity of both flowering plants and anthophilous (flower-loving) insects. Visitation rates to flowers in the continuous area were approximately three times higher than to flowers in habitat fragments. Hand pollination increased seed set in fragmented areas but had no effect on seed set in the continuous areas. In habitat fragments, seed set of flowers did not differ between natural flowers and flowers that had been bagged throughout the reproductive period to prevent cross-pollination. This observation suggests that seeds in the remnant fragments were produced largely through self-pollination. Therefore, fragmentation not only affected the reproductive output but also appeared to change the relative amount of outcrossing as well.

Although habitat fragmentation is a problem, preserving large tracts of a particular vegetation type may not be enough to maintain pollinator populations. Janzen and colleagues (1982) censused euglossine bee populations in parks and reserves in Costa Rica and determined that even within the same park, different habitats vary dramatically in bee diversity. Many of the bee species travel long distances to pollinate plants that do not occur within the habitats in which they were collected. This finding indicates that preservation of diverse patches within an area may be essential to maintain adequate pollinator populations.

Introductions of pollinators. Introductions of pollinators can have both beneficial and detrimental consequences, and have occurred both intentionally and accidentally. Honeybees have spread around the world, where they have become competitors with native bees, birds, and

other pollinators, and bumblebees have also been moved to islands and continents where they did not occur naturally. These introductions have sometimes benefited agriculture, but their consequences for native plants and animals can be deleterious.

The introduction of the honeybee. The honeybee, *Apis mellifera*, has a positive popular image, and it has generally been considered a valuable pollinator. It is native to Europe and has been introduced throughout much of the world for crop pollination. Although honeybees are important for pollination of some crops, the contributions of wild bees on the same crops and the economic value of these other bee species are often ignored. Honeybees have been studied extensively, often at the expense of these other bees. Of the 20,000–30,000 bee species (Neff and Simpson 1993), information on all but a few species is scanty. This information imbalance is a problem because issues of pollination and biodiversity are probably tied more closely to the thousands of wild species than to the domesticated honeybee. In addition, evidence is mounting that honeybees can compete with native pollinators, disrupting natural pollination systems (see below). The introduction of honeybees throughout the world must necessarily alter resource availability for native pollinators, and the impact of honeybee introduction warrants further study.

Honeybees pollinate a wide variety of plants, and they are easy to manage and transport. However, since the 1980s, the number of managed honeybee colonies in the United States has declined as a result of several serious problems: the establishment of bee mites (*Acarapis woodi* and *Varroa jacobsoni*), the establishment of the aggressive African honeybee (*Apis mellifera scutellata*), the reduction of available floral resources outside of agricultural areas, the use of pesticides, and the importation of honey (Torchio 1990). The resulting decline in honeybee availability has produced an increased awareness of the potential role of native bee species in crop pollination and stimulated interest in learning to manage them. Moreover, some researchers have expressed con-

cerns about the wisdom of depending on a single species of bee to pollinate crops (Torchio 1990) and have indicated a growing need to domesticate other pollinating species.

Another problem with honeybees is that, despite their popular image as productive pollinators, they are inefficient pollinators of some crops and many wild plants (O'Toole 1993). Many native North American flowers as well as some crop flowers are not attractive to introduced honeybees and depend on native bees for pollination. Some flowers are the wrong size for honeybees to enter. Bee species range in size from 2 mm to 32 mm—a 3000-fold difference in body mass—and honeybees are approximately 12 mm long. A bee that is too small or too large for a flower will transfer few, if any, pollen grains. Other flowers have small amounts of nectar, making them unattractive to honeybees, and some flowers have specialized mechanisms for pollen release that can deter honeybees. Moreover, flowers may have unusual features that deter honeybees but not their “normal” pollinators. For example, *Zygadenus elegans* (Liliaceae), the death camas, has a nectar that is toxic to honeybees but is eagerly collected by native bees (Tepedino 1979).

Honeybees are also unable to pollinate those plants that rely on “buzz pollination.” Such plants, including several of economic importance, have poricidal anthers (anthers that release pollen from a small hole at the tip rather than splitting open to release pollen) from which pollen is released only when the anther is vibrated at a characteristic frequency. These flowers are pollinated most efficiently by vibratile pollinators. Several groups of bees and a few fly species can buzz pollinate flowers, but this behavior is not in the honeybees' repertoire. Buzz-pollinated crops include cranberries, blueberries, tomatoes, eggplant, and peppers. Some of these plants do not produce nectar and are attractive only to bees foraging for pollen. Others, like blueberry, produce nectar as well as pollen and attract a diverse group of pollinators, including honeybees. A small blueberry stand can be pollinated effectively by native pollinators, but large com-

mercial operations import honeybees in an attempt to ensure fruit set. However, honeybees are not efficient pollinators of blueberry, as was demonstrated one year in New Brunswick, Canada, after a poorly timed pesticide application wiped out many native pollinators of blueberries (O'Toole 1993). To compensate for the loss of native pollinators and ensure fruit set, growers imported colonies of honeybees. However, because honeybees cannot vibrate the anthers, they are less able than vibratile species to access the pollen, and they soon learn to pierce holes in the back of the flowers to rob nectar. These nectar robbers never contact the reproductive parts of the flowers, and fruit set in New Brunswick remained low that year.

Another crop plant that is unsuited to pollination by honeybees is the West Indian cherry, *Malpighia glabra* (Malphiaceae). This tree was introduced to Hawaii as a crop plant (O'Toole 1993) because its fruit is an excellent source of vitamin C. However, fruit set in Hawaii was poor, even after colonies of honeybees were brought in to pollinate the flowers. In this case, the problem was that the honeybee is not attracted to the oil that flowers of the West Indian cherry, like many plants in the Malphiaceae, produce rather than nectar. In its native habitat, the oil is collected by *Centris* bees that simultaneously serve as pollinators.

The introduction of honeybees thus appears to have had a variety of consequences, both unintended and intended. The large number of honeybees in some habitats may make them important competitors for a great diversity of native flower visitors. If native pollinators decline in number, honeybees may not visit or pollinate the same range of flowers, because of their nectar chemistry, small nectar or pollen rewards, flowering phenology, or floral morphology. Although honeybees can be useful in pollination of some crops, native insects can often do as well or better if they are present in sufficient numbers.

Domestication of bees other than the honeybee. Farmers are beginning to appreciate that certain types

of bees may be more effective than honeybees at pollinating specific crops, and some farmers are learning to encourage and manage other alien bee species. For example, honeybees are poor pollinators of alfalfa because alfalfa flowers must be tripped mechanically to discharge their pollen on an insect visitor. After a few experiences of having pollen slapped onto their undersides, honeybees avoid tripping the flowers and instead learn to pierce holes in the backs of the flowers to rob them of nectar. However, cultivation of alternative bee species, such as *Megachile rotundata* (Megachilidae) and *Nomia melanderi* (Halictidae), has resulted in successful pollination of alfalfa (Bohart 1972, O'Toole 1993). *N. melanderi* is a gregarious ground-nesting bee that is native to the western United States. Its management involves providing "bee beds": areas of soil within and adjacent to alfalfa fields that have proper levels of moisture and salinity for nesting. *M. rotundata* is a Eurasian species that nests in premade cavities in wood. Beekeepers provide *M. rotundata* with "bee boards": they predrill holes of the proper diameter into boards that are mounted on stands with wheels. The beekeepers can move these to sites in the field where pollinators are needed. Several other Eurasian pollinators have been suggested for use on alfalfa, a plant native to that region.

Bumblebees have also become pollinators of some crops in regions where they have recently been introduced. In New Zealand, introduced red clover forage is pollinated by three of the four imported European bumblebee species that have become naturalized to the region. The native bees are all short-tongued species that are ineffective pollinators of this crop (O'Toole 1993). Bumblebee culture on a commercial scale has only recently become feasible. Although bumblebees are more expensive to culture than honeybees, it is still economically feasible to domesticate bumblebees for use in greenhouse culture of tomatoes, which are buzz pollinated (Thomson 1993). Domesticated bumblebees are also now being used for greenhouse pollination of strawberries, peppers, eggplant, and squash (Griffiths and Roberts 1996); an unintended but predictable consequence has been the es-

tablishment of feral colonies of alien species (e.g., in Japan, where the European species *Bombus terrestris* has recently been found in the wild).¹

Competition among honeybees and native pollinators. Several studies have indicated that introduced honeybees decrease the foraging success of native pollinators by out-competing them for resources (Ginsburg 1983, Paton 1985, 1993, Pyke and Balzar 1985, Roubik et al. 1986, Schaffer et al. 1979, Sugden and Pyke 1991). A case in point is provided by honeybees in Australia. Honeybees were introduced to Australia approximately 150 years ago, and until recently they were considered beneficial to the native flora. However, new evidence indicates that honeybees may actually be harmful to the native flora: they may displace native pollinators, they may be ineffective at pollinating native flowers, and they may interact in complex ways with native pollinators to reduce the amount and efficiency of pollen transfer (Paton 1993).

Evidence of the detrimental effects of honeybees on a native bee comes from studies in Kosciusko National Park, Australia (Pyke and Balzar 1985, Sugden and Pyke 1991). Both the honeybee and the native bee, *Exoneura asimillima* (Anthophoridae), are highly polylectic (use a wide variety of flowers as food sources), and there is a good deal of overlap in the kinds of flowers that they use. To test for competition among honeybees and the native generalist bee, colonies of honeybees were introduced to alpine areas of the park. After six months, experimental areas contained significantly fewer adult *Exoneura*, although the number of preadult *Exoneura* bees within colonies was the same in experimental areas and in the undisturbed areas that lacked honeybees. Thus, adult *Exoneura* either died or left the area, presumably as a result of competition with honeybees. These findings imply that competition disrupts the natural composition of the community and is likely to have effects on the reproduction of the native vegetation.

¹M. Ono, 1997, personal communication. Tamagawa University, Tokyo, Japan.

Honeybees can also compete with bird pollinators. In communities in Australia where honeybees thrive, Paton (1985) found that honeybees remove one-third to one-half of the available nectar and compete directly with honeyeaters, a group of native pollinating birds. Such areas have reduced honeyeater species diversity and lower floral visitation rates by honeyeaters. Presumably to compensate for the diminished food supply, the honeyeaters increase their territory size. The competition with honeyeaters lowers the pollination success of at least one plant, the largely self-incompatible *Callistemon rugulosus* (Myrtaceae), which both honeyeaters and honeybees visit (Paton 1993). Honeyeaters contact stigmas on more than 50% of visits to the flowers, whereas nectar-gathering honeybees do so on only 4.4% of their visits, and pollen-collecting honeybees do so on 16.7% of their visits. Individual honeybees were watched for 9.9 hours, and not a single between-plant movement was recorded, compared with 7.3 inter-plant movements per hour for honeyeaters (Paton 1993). These differences have consequences for fruit production. Plants enclosed in mesh cages (and which therefore receive only honeybee visits) have significantly lower fruit set than those serviced by birds as well as bees (Paton 1985).

Introduced honeybees in Australia also affect beetle pollinators. Many species of flower-visiting jewel beetles (Buprestidae) in southwestern Australia have suffered from the presence of honeybees. Whereas ten species of beetles could once be observed on a single flowering plant, now only a few may be found (Knowles 1983/4). Since these findings, some reserves have been set aside to help protect the beetles.

Possible effects of introduced honeybees on native bees can be seen in other continents as well. For example, Aizen and Feinsinger (1994a) found an inverse relationship between the number of native bees and the number of honeybees visiting two polyphilic trees (i.e., trees attracting a wide range of flower visitors, such as flies, bees, butterflies, wasps, and beetles) in subtropical dry forests of Argentina. Honeybees were more prevalent in fragmented

areas, whereas wild bees were more common and more diverse in larger tracts of forest. The number of honeybees increased with decreasing fragment size. Aizen and Feinsinger (1994a) suggested that fragmentation could ultimately cause local extinction of some native bee species and replacement by a single species, the introduced honeybee. However, these researchers did not find evidence of direct interactions between native bees and honeybees, and it was not clear that floral resources were in fact limiting native bees in fragmented areas. The shift in pollinators may be more directly related to reduced availability of nesting sites for native bees (a result of habitat fragmentation) and to the foraging patterns of honeybees (whose relative frequency increased with decreasing fragment size). In the small fragments, the polyphilic tree species showed some decline in seed production, despite high levels of visitation by Africanized honeybees, which may have compensated for a decline in visits by native pollinators (Aizen and Feinsinger 1994b). The increase in number of visits by the honeybees was not sufficient to replace the decrease in pollen transfer by native bees, suggesting that honeybees are poorer pollinators. Aizen and Feinsinger (1994b) concluded that monitoring pollination and seed production could provide a useful, integrated measure of the health of disturbed plant communities.

In cases where honeybees do outcompete native bees, why are honeybees more successful? Honeybees appear to be adept at finding and monopolizing nectar- and pollen-rich resources, often at the expense of native bees. Although there is no indication of aggressive interactions among the honeybees and other foragers, temporal and spatial analyses indicate that honeybees dominate large, resource-rich patches of flowers (Ginsburg 1983, Schaffer et al. 1979). In the case of feral Africanized honeybees in South America, the ability to outcompete native bees appears to rely on the capability of Africanized bees to locate and dominate food sources quickly, presumably because of the large number of workers that can

search for food and successfully recruit colony members (Roubik 1980). However, evidence of superior competitive abilities of Africanized bees under natural conditions remains equivocal. Total nectar and pollen collections by native bees do not diminish in the presence of Africanized bees, indicating that native bees may be capable of switching host plants in response to competition (Roubik et al. 1986). Even in cases where there are clear indications that honeybees interfere with the foraging of native pollinators, their effect on the population sizes of native bees is still ambiguous (Aizen and Feinsinger 1994a, Roubik et al. 1986).

Pesticides. Pesticides are another major problem for pollinators. Chemicals applied to crop plants and to rangelands can cause high bee mortality. In the United States, pesticide use has created local problems since the late 1800s, but the problems increased dramatically after World War II, when there was a substantial increase in the use of pesticides on crops, rangelands, and forests (Johansen 1977). Herbicides have also been applied extensively to control weeds in crops and along roadsides, thus reducing the availability of the native wild plants that provide food for pollinators.

Foraging on pesticide-treated plants is a major source of bee mortality, yet honeybees are often expected to pollinate crops that have been treated with pesticides. The susceptibility of bees to chemical poisoning is usually related to their surface area-to-volume ratio. Bumblebees are often more tolerant of pesticides than honeybees because of their smaller surface area-to-volume ratio, and honeybees are in turn more tolerant than most small native bees. Chemical poisoning results in abnormal communication dances and mistakes in indicating distance and direction to food sources, in addition to direct mortality. A mortality rate of 100 dead bees per day in a honeybee colony is considered normal, and only the loss of more than 1000 bees per day is considered serious poisoning (honeybee colonies may contain 40,000–70,000 bees; Johansen 1977).

Bees produce relatively few offspring and invest a large amount of

energy in each. Lab studies of several solitary bee species from North America indicate that under optimal conditions, that is, with plenty of food, a bee will produce 15–20 offspring per year (Tepedino 1979). However, under natural conditions, the number of offspring is likely to be considerably lower because of predation, parasites, and competition. Due to this low fecundity, it may take several years for bee populations to recover after an area has been sprayed with pesticides (Karron 1991); recovery time is even longer if weather conditions are unfavorable or if more pesticide is applied.

One source of pesticides that affects pollinators is the broad-spectrum insecticides used to control grasshoppers on rangelands in the southwestern United States. When grasshoppers are dense, the rangelands are sprayed with these insecticides to save the grasses for cattle forage. The sprays kill many other insects in addition to grasshoppers, including native pollinators. The grasshopper-spraying campaigns (generally from mid-April to late May) overlap the flowering period of a number of endemic rangeland plants that grow among the grasses, several of which are listed as endangered or threatened (Bowlin et al. 1993); they also overlap the period of emergence and active foraging of most native bee species (Peach et al. 1993).

Several rangeland plant species that are listed as endangered depend on insect pollinators for seed set (e.g., *Eriogonum pelinophilum*, Polygonaceae; Bowlin et al. 1993; *Pediocactus sileri*, Cactaceae; Peach et al. 1993), and some of these endangered species show indications of pollinator limitation (e.g., *Purshia subintegra*, Rosaceae; Fitts et al. 1993). At sites where endangered plants are known to occur, an area with a radius of 3 miles around the patch of plants is not sprayed (Fitts et al. 1993). However, the size of this area is arbitrary, and the effectiveness of the procedure is questionable. Relatively little is known about the foraging flight range of most native bees (Peach et al. 1993), and it is not clear how closely this protected area overlaps with the probable nesting site and foraging range of the

endangered plants' pollinators. Many additional plants that are candidates for listing do not receive protection from spraying and may also be affected by the loss of native bees.

Another example of how pesticide application can affect plant reproductive success through its actions on pollinators comes from Thomson et al.'s (1985) studies of forests in New Brunswick, Canada, that were sprayed with Matacil (aminocarb insecticide) to control spruce budworm, *Choristoneura fumiferana* Clem (Tortricidae; Lepidoptera). Native bees in the families Andrenidae, Halictidae, and Anthophoridae and syrphid fly populations were adversely affected by the pesticide; several insects displayed convulsions followed by death. One of the native understory lilies, *Maianthemum canadensis*, showed significant reductions in fecundity, as did a second understory species, *Cornus canadensis* (Cornaceae). Commercial blueberry fields in New Brunswick also suffered reduced fruit set when adjacent forest lands were sprayed with Fenitrothion to control spruce budworm (Kevan 1975).

During pesticide application, honeybee colonies can be removed from fields, but native pollinators may still be exposed to toxins. To minimize harm to these pollinators, insecticides should not be applied during a plant's flowering period. However, many native bees produce multiple broods per summer, and although proper timing of pesticide spraying may ensure pollination of a particular flower species, the net effect of spraying after flowering may be simply to decrease the pollinator population for the subsequent year (Fitts et al. 1993). Bees' hairs easily pick up insecticide dust on flowers and bring it back to their colonies (Johansen 1977), where it can kill larval and adult bees. Another way to minimize harm to pollinators is to avoid spraying pesticides under climatic conditions that enhance toxicity. Hot days and cool nights cause condensation of insecticides on plant leaves, thus prolonging the effects of insecticides and killing more bees. Methods of pesticide application that avoid spraying flowers and foliage are even safer for bees. The use of carbaryl bran baits to

suppress grasshopper populations is being investigated (Peach et al. 1994), but there may be no such alternative application methods for some pesticides.

Degrees of dependence on pollinators

Although we can document threats to pollinators, predicting the actual effect of pollinator loss for a particular plant species is difficult. The significance to a plant of the loss of its pollinators depends on whether the pollination relationship is facultative or obligate (Bond 1994). In assessing the potential threat to a given plant, one must also consider the importance of seed production in the demography of the plant. Some plants thrive as a result of vegetative reproduction and will therefore not be affected by pollinator loss. Others either have large seed banks or are long lived and, thus, may not be in imminent danger of extinction when a pollinator disappears. Rather than strict one-pollinator-one-plant relationships, most plants have multiple pollinators, and most pollina-



Figure 2. A bumblebee queen (*Bombus appositus*) foraging on *Corydalis caseana brandegei* in Colorado near the Rocky Mountain Biological Laboratory. This unusual plant species, a member of the family Fumariaceae that is classified as a state rare plant, is locally abundant but with a very patchy and disjunct distribution. The role of insects in its reproduction is still under study, but the plants require insect visits to set seed and may depend on two species of bumblebees as the only pollinators. Photo: N. Waser, University of California, Riverside.

tors pollinate more than one plant species (Figure 2). Community composition varies among habitats, and what appear to be specialized relationships between a plant species and a pollinator species may change among communities.

The plants most at risk from loss of a pollinator are those that are dioecious and self-incompatible, those that have a single pollinator, and those that propagate only by seeds. Plants form a continuum: at one end are plants that depend strictly on a single pollinator for reproduction, and at the other end are plants that have multiple compensation mechanisms to ensure survival and reproduction. Bond (1994) developed a vulnerability index to rank the threat of extinction of a plant species due to loss of pollinator or disperser mutualisms. The index assesses the vulnerability of a species by considering the following variables: the number of pollinator and disperser species needed, the level of vegetative propagation, whether the species is self-compatible, and

whether the species depends on seedling recruitment. Based on this index, as many as 50% of the 300 species of Proteaceae of the South African Cape can be classified as vulnerable (Bond 1994). Most of these potentially vulnerable species produce few, large seeds, are seed limited, and will not resprout after fire. Many are dioecious. However, Bond (1994) found that many of the species that appear vulnerable have compensatory mechanisms that buffer them in part from pollinator failure: The bird-pollinated species can be pollinated by beetles, and the dioecious ones can be wind pollinated. A greater risk to these plants is the threat imposed by the introduction of an Argentine ant (*Tridomyrmex humilis*) to parts of the region. Many of the species in this area depend exclusively on native ant species for seed dispersal. The introduced ants do not disperse the seeds, and as they displace native ant species, seedling recruitment decreases.

Examples of disrupted pollinator-plant interactions. The repercussions from the disruption of particular pollination systems indicate wide variation in vulnerability among different plants and communities. The following examples illustrate the variation in vulnerability among different types of plants.

- *Freycinetia arborea* (Pandanaeae), the iéie vine, is native to Hawaii. It produces large, colorful inflorescences that are visited by an introduced bird, the Japanese white eye (*Zosterops japonica*), which serves as its major pollinator. Cox (1983) wondered what the original pollinators of this plant might have been and studied the writings of early Hawaiian ornithologists to see whether any rare or extinct endemic birds visited this plant. Finding occasional references indicating that such visits occurred, he examined pollen loads on the feathers of museum specimens of two extinct Hawaiian birds, the Ou (*Psittirostra psittacea*) and *Loxiodes kona* (Drepanididae), and of the endangered Hawaiian crow (*Corvus tropicus*). The two extinct species carried large amounts of *Freycinetia* pollen, and the endangered bird car-

ried moderate amounts. None of these birds carried other species of pollen, and *Freycinetia* pollen was not found on other endemic birds specimens that were tested. Cox (1983) thus suggests that *Freycinetia* received less pollen once these three species began to decline and that the plant then reproduced largely by clonal growth until the Japanese white eye was introduced to Hawaii in 1929. This introduced bird seems to have filled effectively the vacant niche, and once again these plants reproduce sexually.

- Johnson and Bond (1993) conducted research in South African fynbos that indicates that a single species of Satyrid butterfly (*Meneris tulbaghia*) is virtually the only pollinator of a guild of 14 red-flowered plants belonging to four different families (Iridaceae, Orchidaceae, Amaryllidaceae, Crassulaceae). Most of the species require pollinators, and more than half lack compensatory mechanisms to insure their persistence in the absence of pollinators, although some have bulbs or produce hundreds of tiny seeds when they are pollinated. Most of the species are rare, possibly because of this need for a specific pollinator. At least one of these species, *Disa uniflora* (Orchidaceae), sets significantly less seed in habitats that the butterfly does not favor, as a direct result of low-visitation rates (Johnson and Bond 1992).

- *Thelymitra epipactoides* is an endangered orchid found on the coastal heaths of southeastern Australia (Cropper and Calder 1990). Although it is visited by many bee species, it appears to be pollinated largely by bees of the genus *Nomia* (Halictidae). The flowers produce a sweet scent but do not offer nutritional rewards; thus, the relationship is one of "deceit pollination." Extant populations of the orchid produced no seeds, and few pollinia had been removed from the flowers, although a small number of *Nomia* bees were observed carrying pollinia (Cropper and Calder 1990). The rarity of the plant has been blamed on orchid lovers who collect the plants and on general habitat destruction. However, Cropper and Calder (1990) suggest that habitat management and a consequent reduction in fires has contributed to the plant's

rarity. The lack of fires results in a climax community with low species diversity and with a decreased total floral abundance. Because *Nomia* is a polylectic species, the reduced floral abundance probably makes the habitat less attractive to pollinators, resulting in poor pollination.

- A rare fynbos shrub of the African Cape, *Ixianthes retzioides* (Scrophulariaceae), grows in rapids and waterfalls, with its roots anchored in rock crevices (Steiner 1993). Its flowers produce oil as a pollinator attractant. Its nearest relatives (*Bowkeria* and *Anastrabe*) also have oil flowers and are pollinated by bees of the genus *Rediviva*. Female bees collect the floral oil to provision nests or as a precursor for a material for lining nest cells. These same bees visit other flowers for nectar. Over the course of four years, Steiner (1993) observed only a few insects visiting the flowers (a honeybee, a halictid bee, and one small unidentified bee), and fruit set was extremely low. However, when the flowers were hand pollinated, they set seven times as many fruits. Based on the oil composition, flower morphology, and size of the plant, Steiner (1993) suggests that it is adapted to pollination by a large, oil-collecting, specialist bee, although no oil-collecting bees have been observed visiting the flowers. An undescribed bee of the appropriate size, morphology, and phenology—probably of the genus *Rediviva*—has been collected at three sites outside the known range of the plant. Despite this apparent "uncoupling" of plant and pollinator through loss of the local pollinator population, *Ixianthes* persists through vegetative propagation.

Cascade effects. In some systems, factors that affect a pollinator have the potential to create a cascade of events affecting multiple species. The following examples illustrate this point:

- Male euglossine bees pollinate many neotropical orchids that are obligate outcrossers. The male bees have brushes on their front legs that are used to collect fragrances and a modified hind leg for scent storage. They visit the flowers to collect scents, which appear to be important for mating success. Approxi-

mately half of the euglossine-orchid mutualisms involve a single bee species, and half involve from 2 to 12 euglossine species per orchid species (Roubik 1992). In contrast to males, female euglossines normally travel long distances along predictable routes, visiting widely dispersed woody plants that occur at low densities in the tropical forest. As the number of these trees has decreased due to lumbering, grazing, and development, bee nesting sites have been destroyed and the total number of bees has decreased. Female bees have shifted to feeding on weedy shrubs in disturbed sites, and it is unlikely that they will continue to serve as reliable outcrossers of distantly spaced flowering trees. Reduced visitation by female bees will further decrease the chances of survival of the tree species, and the relationship will spiral into decline. The fates of the orchids, the bees, and the native woody plants are all intimately connected (Janzen 1974).

- Fig trees are keystone species in tropical communities. For example, in Cocha Cashu, Peru, several primate species, procyonids, marsupials, toucans, and other birds depend on figs as a staple food (Terborgh 1986). Worldwide, there are approximately 800 species of fig, each of which depends on a unique species of wasp for pollination. The fig wasps are tiny, approximately 1 mm in length. Asynchronous flowering is essential for the year-round survival of the fig wasps, which die if no flowers are available within a few days after hatching (Thomson et al. 1991). Thus, a reduction in tree numbers could negatively affect wasp population viability; simulation models suggest that a minimum viable population size of 300 trees is needed to maintain a wasp population (Thomson et al. 1991). If wasp pollinator populations are lost, then the food base of many species could collapse (LaSalle and Gauld 1993).

Preservation of plant-pollinator systems

Management of pollination systems is a relatively new and untried strategy for their conservation. For both plants and pollinators, preservation

Figure 3. A bumblebee queen (*Bombus occidentalis*) visits a male catkin to collect pollen. Willow flowers (*Salix* species) are important sources of nectar and pollen for flower visitors early in the spring. Willows provide the pollen required for some species of bumblebee to initiate nests but are soon replaced in the bees' diets by a series of later-blooming species.



may require little more than protection or management of appropriate habitat. For example, leaving unplowed strips of land between agricultural fields may encourage nesting by native bees, such as bumblebees. Similarly, fragmentation of forests may result in decreased pollination and seed production (e.g., Aizen and Feinsinger 1994b), and protection of forest habitat may help to prevent such a decline. Preservation of habitat for plants that provide nectar and pollen throughout the season during which a pollinator species is active may also be important in conserving pollination systems. To ensure provision of a season-long supply of nectar and pollen, knowledge of the phenology of flowering is essential (Figure 3). In other cases, more active measures, such as controlled burns, may be required to exclude woody plants and maintain communities of herbaceous plants to provide appropriate floral resources for pollinators.

Reintroductions of locally extinct populations of plants or pollinators are also a possible strategy for reestablishing plant-pollinator relationships. For example, an effort is underway in Japan to restore native bumblebee pollinators to an area where seed production by a rare primrose species, *Primula*

sieboldii, has been greatly reduced.² In the absence of a native pollinator, it may be possible, as an interim measure, to use hand pollination for seed production. In those cases in which introduced honeybees have outcompeted native pollinators, resulting in reduced seed production by native plant species, then it may be possible to reduce the density of the introduced bees by removing apiaries or trapping feral colonies.

The biology of small populations presents special problems for management of plant-pollinator systems. Small plant populations may have reduced seed set because of a lower density of flowering plants, genetic effects such as inbreeding depression, or failure to set seed due to incompatibility problems. For example, DeMauro (1993) found that a sand dune population of the rare species *Hymenoxys acaulis* (Asteraceae) was

²J. Thompson, 1995, personal communication. State University of New York, Stony Brook, NY.

effectively extinct because it contained only a single self-compatibility type and could no longer produce seeds. In this case, the population could potentially be rescued—albeit at the cost of introducing foreign genes from another population—by importing plants of a compatible mating type. Management of habitat to prevent fragmentation of plant populations is another means to forestall reproductive problems resulting from small population size.

Extinctions of ecological interactions may be more difficult to notice than extinctions of individual species. One of the partners may persist for several years after the other is gone because of long-lived individuals or compensation mechanisms (Janzen 1974). Predicting the effects of loss of a particular pollinator is extremely difficult, but it is important to remember that no species exists in isolation. Each is part of an ecological web, and as we lose more and more pieces of that web, the remaining structure must eventually collapse.

References cited

Aizen MA, Feinsinger P. 1994a. Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine Chaco Serrano. *Ecological Applications* 4: 378–392.

_____. 1994b. Forest fragmentation, pollination, and plant reproduction in a chaco dry forest, Argentina. *Ecology* 75: 330–351.

Bohart GE. 1972. Management of wild bees for the pollination of crops. *Annual Review of Entomology* 17: 287–312.

Bond WJ. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philosophical Transactions of the Royal Society, London B Biological Sciences* 344: 83–90.

Bowlin WR, Tepedino VJ, Griswold TL. 1993. The reproductive biology of *Eriogonum pelinophilum* (Polygonaceae). Pages 296–302 in Sivinski R, Lightfoot K, eds. *Southwestern rare and endangered plants*. Miscellaneous publication nr 2. Santa Fe (NM): New Mexico Forestry and Resources Conservation Division.

Buchmann SL, Nabhan GP. 1996. *The forgotten pollinators*. Washington (DC): Island Press.

Cox PA. 1983. Extinction of the Hawaiian avifauna resulted in a change of pollinators for the iieie, *Freycinetia arborea*. *Oikos* 41: 195–199.

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 Systematics and Evolution* 170: 11–27.

Darwin CR. 1859. *On the origin of species by means of natural selection*. London (UK): John Murray.

DeMauro MM. 1993. Relationship of breeding system to rarity in the lakeside daisy (*Hymenoxys acaulis* var. *glabra*). *Conservation Biology* 7: 221–223.

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). Pages 268–359 in Sivinski R, Lightfoot K, eds. *Southwestern rare and endangered plants*. Miscellaneous publication nr 2. Santa Fe (NM): New Mexico Forestry and Resources Conservation Division.

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. Pages 83–114 in LaSalle J, Gauld ID, eds. *Hymenoptera and biodiversity*. Oxon (UK): C.A.B. International.

Ginsburg HS. 1983. Foraging ecology of bees in an old field. *Ecology* 64: 165–175.

Griffiths D, Robberts EJ. 1996. Bumble bees as pollinators of glasshouse crops. Pages 33–39 in Matheson A, ed. *Bumble bees for pleasure and for profit*. Cardiff (UK): International Bee Research Association.

Janzen DH. 1974. The deflowering of Central America. *Natural History* 83: 49–53.

Janzen DH, DeVries PJ, Higgins ML, Kimsey LS. 1982. Seasonal and site variation in Costa Rican euglossine bees at chemical baits in lowland deciduous and evergreen forests. *Ecology* 63: 66–74.

Jennersten O. 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. *Conservation Biology* 2: 359–366.

Johansen CA. 1977. Pesticides and pollinators. *Annual Review of Entomology* 22: 177–192.

Johnson SD, Bond WJ. 1992. Habitat dependent pollination success in a Cape orchid. *Oecologia* 91: 455–456.

_____. 1993. Red flowers and butterfly pollination in the fynbos. Pages 137–148 in Arianoutsou M, Groves RH, eds. *Plant animal interactions in Mediterranean-type ecosystems*. Dordrecht (the Netherlands): Kluwer Academic Publishers.

Karron JD. 1991. Patterns of genetic variation and breeding systems in rare plant species. Pages 87–98 in Falk DE, Holsinger KE, eds. *Genetics and conservation of rare plants*. New York: Oxford University Press.

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. *Biological Conservation* 7: 301–309.

Knowles D. 1983/4. Flying jewels. *Geo* 5: 46–57.

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: 446–450.

LaSalle J, Gauld ID. 1993. Hymenoptera: their diversity, and their impact on the

diversity of other organisms. Pages 1–26 in LaSalle J, Gauld ID, eds. *Hymenoptera and biodiversity*. Oxon (UK): C.A.B. International.

Levin DA. 1971. The origin of reproductive isolating mechanisms in flowering plants. *Taxon* 20: 91–113.

Nabhan GP. 1996. The parable of the poppy and the bee. *Nature Conservancy* 46: 11–15.

Neff JL, Simpson BB. 1993. Bees, pollination systems and plant diversity. Pages 143–168 in LaSalle J, Gauld ID, eds. *Hymenoptera and biodiversity*. Oxon (UK): C.A.B. International.

O'Toole C. 1993. Diversity of native bees and agroecosystems. Pages 169–196 in LaSalle J, Gauld ID, eds. *Hymenoptera and biodiversity*. Oxon (UK): C.A.B. International.

Paton DC. 1985. Food supply, population structure, and behaviour of New Holland honeyeaters *Phylidonyris novaehollandiae* in woodlands near Horsham, Victoria. Pages 222–230 in Keast A, Recher HF, Ford H, Saunders D, eds. *Birds of eucalypt forests and woodlands: ecology, conservation, and management*. Sydney (Australia): Royal Australian Ornithologists Union and Surrey Beatty & Sons.

_____. 1993. Honeybees in the Australian environment. *BioScience* 43: 95–103.

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). Pages 309–333 in Sivinski R, Lightfoot K, eds. *Southwestern rare and endangered plants*. Miscellaneous publication nr 2. Santa Fe (NM): New Mexico Forestry and Resources Conservation Division.

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? *Journal of Economic Entomology* 87: 311–317.

Pyke GH, Balzer L. 1985. The effects of the introduced honey bee (*Apis mellifera*) on Australian native bees. Occasional paper nr 7. Sydney (Australia): New South Wales National Parks Wildlife Service.

Roubik DW. 1980. Foraging behavior of competing Africanized honeybees and stingless bees. *Ecology* 61: 836–845.

_____. 1992. Loose niches in tropical communities: why are there so few bees and so many trees? Pages 327–354 in Hunter MD, Ohgushi T, Price P, eds. *Effects of resource distribution on animal-plant interactions*. New York: Academic Press.

Roubik DW, Moreno JE, Vergara C, Wittmann D. 1986. Sporadic food competition with the African honey bee: projected impact on neotropical social bees. *Journal of Tropical Ecology* 2: 97–111.

Schaffer WM, Jensen DB, Hobbs DE, Gurevitch J, Todd JR, Schaffer MV. 1979. Competition, foraging energetics and the cost of sociality in three species of bees. *Ecology* 60: 976–987.

Snow AA, Spira TP. 1991. Pollen vigor and the potential for sexual selection in plants. *Nature* 352: 796–797.

Stebbins GL. 1979. Rare species as examples of plant evolution. Pages 113–118 in *Great Basin naturalist memoirs nr 3: the endan-*

- gered species: a symposium; 7–8 Dec 1978. Provo (UT): Brigham Young University.
- Steiner KE. 1993. Has *Ixianthes* (Scrophulariaceae) lost its special bee? *Plant Systematics and Evolution* 185: 7–16.
- Sugden EA, Pyke GH. 1991. Effects of honey bees on colonies of *Exoneura asimillima*, an Australian native bee. *Australian Journal of Ecology* 16: 171–181.
- Tepedino VJ. 1979. The importance of bees and other insect pollinators in maintaining floral species composition. Pages 39–150 in Great Basin naturalist memoirs nr 3: the endangered species: a symposium; 7–8 Dec 1978. Provo (UT): Brigham Young University.
- Terborgh J. 1986. Keystone plant resources in the tropical forest. Pages 330–344 in Soulé ME, ed. *Conservation biology*. Sunderland (MA): Sinauer.
- Thomson JD. 1993. The queen of forage and the bumblebee revolution: a conference with an attitude. *Trends in Ecology & Evolution* 8: 41–42.
- Thomson JD, Plowright RC, Thaler GR. 1985. Matacil insecticide spraying, pollinator mortality, and plant fecundity in New Brunswick forests. *Canadian Journal of Botany* 63: 2056–2061.
- Thomson JD, Herre EA, Hamrick JL, Stone JL. 1991. Genetic mosaics in strangler fig trees: implications for tropical conservation. *Science* 254: 1214–1216.
- Torchio PF. 1990. Diversification of pollination strategies for U.S. crops. *Environmental Entomology* 19: 1649–1656.
- Vinson SB, Frankie GW, Barthell J. 1993. Threats to the diversity of solitary bees in a neotropical dry forest in Central America. Pages 53–82 in LaSalle J, Gauld ID, eds. *Hymenoptera and biodiversity*. Oxon (UK): C.A.B. International.
- Williams CS. 1995. Conserving Europe's bees: why all the buzz? *Trends in Ecology & Evolution* 10: 309–310.
- Williams PH. 1986. Environmental change and the distributions of British bumble bees (*Bombus* Latr.). *Bee World* 67: 50–61.



Support America's colleges. Because college is more than a place where young people are preparing for their future. It's where *America* is preparing for *its* future.

If our country's going to get smarter, stronger—and more competitive—our colleges and universities simply must become a national priority.

It's an investment we all share in. Government. Private citizens. And the business community. After all, the future of American business depends on it.

So help America prepare for the future with a corporate gift to the college of your choice—and you'll know your company has done its part.

**Give to
the college of
your choice.**