
Commissioned Paper: A Statement by the Society for Conservation Biology

In a continuing effort to address contemporary conservation issues in a scholarly and rigorous fashion, the Board of Governors of the Society for Conservation Biology in 1997 approved a process by which a series of Commissioned Papers will be developed and published. Drawing on the Articles of Incorporation of SCB, which charge the Society to "disseminate scientific, technical, and management information through meetings, publications, and other media" and to "advance and articulate the Society's position on matters of public policy," this process is intended to formulate SCB positions on difficult issues relevant to the scientific basis for conservation. Those positions are made clear and explicit through publication of Commissioned Papers in this journal and may be used by the Society officers, Board of Governors, and members to guide activities of the society, synthesize and communicate the findings of conservation biology to the interested public, and inform decision makers of the Society's scientific insights into issues relevant to public policy. The authority for such papers arises from the bylaws of the Society, which authorize the Policy and Resolutions Committee to develop "positions for the Society on issues related to conservation biology or policy issues where the scientific or management expertise of the Society will be of value" and to adopt "a protocol for the development of position statements and position papers." Details of the process by which such papers are developed and approved by the Society were published in the SCB newsletter of November 1997 (Vol. 4, No. 4) and should be sought for further details.

In this, the first SCB Commissioned Paper, Gary Paul Nabhan and co-authors address an emerging and critically important issue: worldwide pollinator declines and their possible consequences for biodiversity conservation and agricultural stability. We plan to follow this with several Commissioned Papers each year on a broad scope of topics in an ongoing effort to clearly formulate SCB positions and influence public policy. The President and Board of Governors welcome suggestions from members for appropriate topics and will seek member input in writing these papers.

Gary K. Meffe

The Potential Consequences of Pollinator Declines on the Conservation of Biodiversity and Stability of Food Crop Yields

Gordon Allen-Wardell, BeeMaster, Inc., 1665 E. 18th St., #209, Tucson, AZ 85719, U.S.A.

Peter Bernhardt, Department of Biology, St. Louis University, 3507 LaClede, St. Louis, MO 63101-2010, U.S.A.

Ron Bitner, International Pollination Systems, 16645 Plum Rd., Caldwell, ID 83605, U.S.A.

Alberto Burquez, Instituto de Ecologia, UNAM, Apartado Postal 1354, Hermosillo, Sonora 83000, Mexico

Stephen Buchmann, USDA/ARS, 2000 E. Allen Rd., Tucson, AZ 85719, U.S.A.

James Cane, USDA/ARS Bee Biology and Systematics Lab, Utah State University, Logan, UT 84322-5310, U.S.A.

Paul Allen Cox, National Tropical Botanical Garden, P.O. Box 340, Lawai, Kauai, HI 96765, U.S.A.

Virginia Dalton, Science Department, Pima College West, Desert Vista, 5901 South Calle Santa Cruz, Tucson, AZ 85709-6000, U.S.A.

Peter Feinsinger, Department of Biology, Northern University University, 5315 N. Copeland, Flagstaff, AZ 86004, U.S.A.

Mrrill Ingram, Arizona-Sonora Desert Museum, 2101 North Kinney Road, Tucson, AZ 85743, U.S.A.

David Inouye, Department of Sustainable Development and Conservation Biology, University of Maryland, College Park, MD 20742, U.S.A.

C. Eugene Jones, Department of Biological Services, California State University at Fullerton, Fullerton, CA 92831, U.S.A.

Kathryn Kennedy, U.S. Fish and Wildlife Service, 17011 Burnet Rd., Suite 200, Austin, TX 78716, U.S.A.

Peter Kevan, Department of Environmental Biology, University of Guelph, Guelph, Ontario N1G 2W1, Canada

Harold Koopowitz, Department of Biology, University of California, Irvine, CA 92717, U.S.A.

Rodrigo Medellin, Instituto de Ecologia, UNAM, Ciudad Universitaria, Apartado Postal 70-275 D.F., 04510, Mexico

Sergio Medellin-Morales, Terra Nostra, Apartado Postal 636, Ciudad Victoria, Tamaulipas 887040, Mexico

*Gary Paul Nabhan, Arizona-Sonora Desert Museum, 2021 North Kinney, Tucson, AZ 85743, U.S.A.

*Address correspondence to primary contact/editor, Gary Paul Nabhan, Arizona-Sonora Desert Museum, 2021 N. Kinney Road, Tucson, AZ 85743-8918, email fpollen@azstarnet.com

Paper submitted April 9, 1997; revised manuscript accepted October 1, 1997.

Bruce Pavlik, Department of Biology, Mills College, Oakland, CA 94610, U.S.A.
 Vincent Tepedino, USDA/ARS, Bee Biology and Systematics Lab., Utah State University, Logan, UT 84322-5310, U.S.A.
 Phillip Torchio, USDA/ARS, Bee Biology and Systematics Lab., Utah State University, Logan, UT 84321, U.S.A.
 Steve Walker, Bat Conservation International, 500 North Capital of Texas Highway, Austin, TX, U.S.A.

Endorsers: Arizona-Sonora Desert Museum; Bat Conservation International; Committee for Sustainable Agriculture; Community Alliance with Family Farmers; International Pollination Systems; Maine Organic Farmers and Gardeners Association; National Wildflower Research Center; Seacology Foundation; Society for Conservation Biology; Society for Ecological Restoration; Sonoran Arthropod Studies Institute; Terra Nostra, A.C.; and University of Maryland Department of Sustainable Development and Conservation Biology

Abstract: *Following reports of dramatic declines in managed and feral honey bees from nearly every region of North America, scientists and resource managers from the U.S., Mexico, and Canada came together to review the quality of the evidence that honey bees as well as other pollinators are in long-term decline and to consider the potential consequences of these losses on the conservation of biodiversity and the stability of the yield of food crops. These experts in pollination ecology confirmed that the last 5 years of losses of honeybee colonies in North America leave us with fewer managed pollinators than at any time in the last 50 years and that the management and protection of wild pollinators is an issue of paramount importance to our food supply system. Although there are conclusive data that indicate 1200 wild vertebrate pollinators may be at risk, data on the status of most invertebrate species that act as pollination agents is lacking. The recommendations from a working group of over 20 field scientists, presented here, have been endorsed by 14 conservation and sustainable agriculture organizations, research institutes, and professional societies, including the Society for Conservation Biology. Among the most critical priorities for future research and conservation of pollinator species are (1) increased attention to invertebrate systematics, monitoring, and reintroduction as part of critical habitat management and restoration plans; (2) multi-year assessments of the lethal and sublethal effects of pesticides, herbicides, and habitat fragmentation on wild pollinator populations in and near croplands; (3) inclusion of the monitoring of seed and fruit set and floral visitation rates in endangered plant management and recovery plans; (4) inclusion of habitat needs for critically-important pollinators in the critical habitat designations for endangered plants; (5) identification and protection of floral reserves near roost sites along the "nectar corridors" of threatened migratory pollinators; and (6) investment in the restoration and management of a diversity of pollinators and their habitats adjacent to croplands in order to stabilize or improve crop yields. The work group encourages increased education and training to ensure that both the lay public and resource managers understand that pollination is one of the most important ecological services provided to agriculture through the responsible management and protection of wildland habitats and their populations of pollen-vectoring animals and nectar-producing plants.*

Consecuencias Potenciales de la Disminución de Polinizadores en la Conservación de la Biodiversidad y la Estabilidad en la Producción de Cosechas de Alimentos

Resumen: *Debido a los constantes reportes de disminuciones dramáticas de abejas productoras de miel tanto manejadas como silvestres en casi todas las regiones de Norteamérica, científicos y manejadores de recursos de Estados Unidos, México y Canadá se reunieron para revisar la calidad de las evidencias de que las abejas, así como otros polinizadores se encuentran en una disminución a largo plazo y para considerar las consecuencias potenciales de estas pérdidas en la conservación de la biodiversidad y la estabilidad de las cosechas de alimentos. Estos expertos en ecología de la polinización confirmaron que los últimos cinco años de pérdidas de colonias de abejas en Norteamérica nos ubican con menos polinizadores manejados que en ningún otro momento en los últimos 50 años y que el manejo y protección de polinizadores silvestres es un aspecto de suma importancia para nuestro sistema de abastecimiento de alimentos. A pesar de que existen datos concluyentes que indican que 1200 polinizadores vertebrados silvestres podrían encontrarse en riesgo, se carece de datos sobre la situación de la mayoría de las especies de invertebrados que actúan como polinizadores. Las recomendaciones de un grupo de trabajo de más de 20 científicos, presentadas aquí, han sido respaldadas por 14 organizaciones de conservación y agricultura sustentable, institutos de investigación y sociedades de profesionistas incluyendo la Sociedad para la Biología de la Conservación. Entre las prioridades más críticas de investigación y conservación de especies de polinizadores se encuentran; 1) incrementar el enfoque en sistemática de invertebrados, monitoreo y reintroducción como parte del manejo de hábitat crítico y planes de restauración; 2) evaluaciones de varios años de los efectos letales y subletales de pesticidas, herbicidas y la fragmentación del hábitat en las poblaciones silvestres de polinizadores dentro y alrededor de las*

tierras de cosechas; 3) inclusión del monitoreo de semillas y frutas y las tasas de visita en los planes de manejo y recuperación de plantas; 4) inclusión de las necesidades de hábitat para polinizadores críticamente importantes en las designaciones de hábitat crítico para plantas amenazadas; 5) identificación y protección de reservas florales cerca de sitios de percha a lo largo de "corredores de néctar" de polinizadores migratorios amenazados; y 6) inversión en la investigación y manejo de una diversidad de polinizadores y sus hábitats adyacentes a sitios con cosechas para poder estabilizar e improvisar la producción de las cosechas. El grupo de trabajo hace un llamado para estimular un incremento en educación y entrenamiento para asegurar que tanto el público como los manejadores de recursos entiendan que la polinización es uno de los servicios ecológicos más importantes aportados a la agricultura a través del manejo responsable y la protección de hábitats silvestres y de sus poblaciones de animales vectores de polen y plantas productoras de néctar.

Introduction

The numbers of feral and managed honey bee colonies have dropped precipitously in the United States in the last several years—by 25% since 1990—with radical implications for the pollination of both wild plant communities and agricultural crops (Buchmann & Nabhan 1996; Ingram 1996). Such declines of pollinators are not limited to honey bees in North America. Worldwide, nearly 200 species of wild vertebrate pollinators may be on the verge of extinction (Nabhan 1996), along with an untold number of invertebrate pollinators (Matheson et al. 1996). A work session was convened to address the growing concern that failure to confront the declines in populations of animals providing pollination services could have major long-term economic and ecological implications. Currently, government statistics on pollinating animals focus exclusively on managed honey bees, so there is no clear documentation of global population trends for non-*Apis* bees or other pollinating animal species (e.g., bats, beetles, birds, butterflies, flies, moths, wasps, and some primates). Neither has there been sufficient research into the impacts of pollination problems nor into providing protection to pollinator species to avert further agricultural and ecological impacts (Kearns & Inouye 1997). As biologists, we value diversity and believe that global problems require global solutions. Our overarching goal should be to benefit the diverse biological and human communities dependent on the health of the myriad of species of animals providing pollination services. We focused on the following issues: (1) establishing a consensus regarding the geographic extent and magnitude of declines in invertebrate and vertebrate pollinator species and of the resulting declines in pollination services to native floras and crops; (2) identifying significant gaps in our knowledge regarding the relative degree of disruption of relationships between pollinators, crops, and native plants; and (3) making recommendations for monitoring, sustaining, or restoring pollinator populations.

Invertebrates

Honey Bees (*Apis mellifera*)

Managed and feral European honey bees throughout the United States and other countries, such as France and Germany, are experiencing major population declines as the result of introduced parasitic mites, pesticide misuse, bad weather, or threats from Africanized honey bees (Matheson et al. 1996). Data are unequivocal for managed colonies in the United States, where colony numbers declined from 2.5 million in 1995 to only 1.9 million by late 1996 (USDA National Agricultural Statistics Services 1997). Quantitative data for feral colonies are available only regionally, but drastic losses are known (Loper 1995). Parasitic varroa and tracheal mites are believed to be the primary cause of these declines in wildlands. But the available data on the demise of feral colonies have been collected by only a few researchers from geographically scattered research plots and are not comprehensive. Data on honey bee colonies in the United States have historically been taken by state apiarists, but, due to budget cuts, few of those positions remain. Today, few state departments of agriculture collect and analyze data even on managed honey bee colonies.

The known consequences of these honey bee declines on pollination services are scarcely documented for agricultural crops, let alone for wild plant populations of concern. In several states the lack of pollination by honey bees has already been blamed for reduced crop yields, but the magnitude of loss related directly to honey bee declines is poorly documented. Economic production cost increases have been documented for some major agricultural crops, such as California almonds, in response to shortfalls in the availability of mobile honey bee colonies (Watanabe 1994). Impacts may in fact be felt more strongly in home gardens and on small farms that do not rent managed honey bees but that have relied on wild bee populations for pollination. Although the economic value of managed honey bees to U.S. agricul-

ture has been routinely estimated, it needs to better reflect honey bees' contributions to crop pollination and fruit yields relative to that of other pollinators (Southwick & Southwick 1992; Nabhan & Buchmann 1997).

A nationally coordinated effort to address the issues of honey bee declines is very much needed; it should include

- multidisciplinary research on the long-term impacts of mites and diseases affecting all honey bees;
- determinations of the pollination efficiency and value of Africanized bees, which are already major crop pollinators for cultivated plants in North America;
- monitoring changes in the density of feral honey bee colonies using the same methodologies at fixed sampling areas in various regions of North America;
- research on the extent to which sublethal doses of pesticides disrupt the behavior, reproduction, and immune responses of honey bees to mites and diseases and other pests;
- programs to reduce pesticide misuse, such as better regulations regarding warnings on labels of chemicals toxic to bees, and other educational efforts aimed at farmers and pesticide applicators;
- educational programs for farm managers, state highway departments, and park managers to encourage sowing of bee forage plants to provide nectar and pollen so that beekeepers' livelihoods can benefit from sound land management policies and practices;
- promotion of seed mixes and cover crops for land reclamation that are "pollinator friendly."

Non-*Apis* Bees and Other Invertebrate Pollinators

Moths, flies, wasps, bees, beetles, butterflies, and other invertebrates are critically important for ensuring the effective pollination of both cultivated and wild plants (Free 1993; Roubik 1995; Buchmann 1996). Although some population declines have been documented for non-*Apis* bees—those solitary bees that do not live in human-made hives (O'Toole 1993; Aizen & Feinsinger 1994)—we are less confident of the pervasiveness of population declines for other insect pollinators. Documentation of a decline in effective cross-pollination as a result of invertebrate declines is available for only a few specific situations (Suzan et al. 1994; Washitani 1996). These and other case studies were accomplished in agricultural and natural settings, where crops and native plants were shown to suffer reduced fruit- and seed-set, in part as a result of pollinator scarcity (Tepedino et al. 1996). The existing examples are largely regional or case-specific, but they are nevertheless highly indicative of more general global problems and should not be considered "merely anecdotal" (Nabhan & Buchmann 1996).

There are striking gaps in our knowledge of the interactions between invertebrate pollinators and the plants they

visit in search of food (Kearns & Inouye 1997). Butterflies, for example, whose taxonomy and biogeography are perhaps better known than other insects, are important pollinators, yet their exact roles as primary or secondary pollinators remain relatively unknown and unappreciated. We also lack understanding of the variability in the abundance and diversity of pollinators through space and time. Finally, economic analyses of the value of pollination services for field and forest crops have never adequately taken into account wild invertebrate pollinators. Honey bees are typically given sole credit for the pollination of the 100–150 major crops grown in the United States, but native bees, butterflies, moths, and flies play roles for these crops that are often as or more significant than those of managed honey bees (Roubik 1995; Buchmann & Nabhan 1996).

To conserve invertebrate pollinators, we see a need for

- increased funding for studies of a diversity of economically important plant-pollinator relationships, including analyses of the life histories and the ecological and economic roles of flying insects and their pollen or nectar sources;
- discerning the patterns of interactions among pollinators and plants in exemplary biomes (e.g., rainforests, grasslands, deserts, temperate forests) with respect to community structure, degree of generalization, or specialization of interactions, and ecosystem health;
- long-term monitoring protocols for use in protected areas that allow the collection of baseline data to establish benchmarks in order to assess changes in the diversity and abundance of pollinators through time;
- a greater investment in training invertebrate systematists in order to overcome the lack of taxonomic expertise (devoted to the curation of museum collections and the field sampling of invertebrates);
- multi-year assessments of sublethal and lethal effects of pesticides and herbicides on wild invertebrate pollinator populations in and near croplands;
- development of an endangered invertebrate pollinator list (i.e., an IUCN Red Book) for national, continental, and global domains;
- educational campaigns to encourage greater awareness of which species serve as native pollinators for wild and cultivated plants;
- development of invertebrate pollinator translocation protocols for ecological restoration projects (Montalvo et al. 1997).

Vertebrates

Bats

Bats are important pollinators in biotic communities in the tropics, deserts, and many oceanic islands (Fleming

1993). For example, in arid regions of South and North America, most species of columnar cacti and many species of agave are pollinated by bats (McGregor et al. 1962; U.S. Fish and Wildlife Service 1994; Valiente-Banuet et al. 1995; Petit & Pors 1996). On oceanic islands such as Samoa, bats pollinate the majority of the dominant rain forest canopy trees (Cox et al. 1991). Many economically important plants are bat-pollinated, including durians, neem trees, wild bananas, timber species of eucalyptus, and several species of palms (Fujita 1991).

There is unequivocal evidence documenting dramatic declines for individual species and populations of pollinating bats. At least 45 species of bats are of global conservation concern, including 9 species presumed extinct in the wild (Nabhan 1996). Whereas bat pollinators are endangered in Australia, Africa, North America, South America, Central America, and Asia, hardest hit are species of microchiroptera restricted to individual islands or archipelagos (Cox et al. 1991). These areas also happen to be places where other pollinators are scarce or absent. There remains a lack of definitive studies of pollinating bat species on large continental land masses, research similar to the exhaustive study recently done on island populations of flying foxes (Mickleburgh et al. 1992).

For megachiroptera (fruit bats and flying foxes), the gravest threats in order of importance are hunting, deforestation, introduction of exotic predators, and unpredictable environmental disturbances such as cyclones. The most serious threats to microchiroptera are habitat fragmentation and human destruction or disturbance of roosting caves and mines. Less understood but also believed to be important are the effects of environmental contaminants on bat populations (Clark 1981; Sutton & Wilson 1983).

To make accurate predictions regarding the ultimate consequences of these declines on plant reproduction, conservation biologists require better assessments of the long-term contribution of bat pollination at the community level. Population monitoring techniques for pollinating bats (including studies of roosting behavior, foraging strategies, determination of home ranges, and the importance of "nectar corridors" in migration) are still in their infancy (Federal Register 1988), although technologies such as radio tracking offer innovative opportunities for study.

Several steps are necessary to further the management and conservation of bats. First we need to pursue long-term monitoring studies of nectar-feeding bat populations documenting (1) changing geographical patterns of species distributions (Koopman 1981), (2) changing pollinator densities and the extent to which they are due to anthropogenic effects versus environmental fluctuations, and (3) ecosystem level patterns of plant-bat relationships. Second, we need to enact legislation and management protocols to protect vulnerable bat species and their habitats (especially species in the South Pacific basin) by reducing the impacts of grazing, mining, logging, and pesticide use on endangered pollinating bats. Fi-

nally, we need to increase support for community-level education on the economic and cultural values of bat pollination and for the development of feasible conservation strategies for land managers.

Non-flying Mammals

Although a diversity of non-flying mammals visit the flowers of tropical trees and shrubs, their relative roles in effective pollination are not well known. Several species of lemurs, monkeys, olingos, kinkajous, and tree squirrels may be effective in cross-pollinating plants (Janson et al. 1981; Mittermeier et al. 1994). Unfortunately, at least 36 species of these non-flying mammal pollinators may be at risk of extinction in the wild due to forest destruction, habitat fragmentation, changes in canopy structure, and hunting (Nabhan 1996). There is unequivocal evidence of declines in these species, but the effects of their diminished activity as pollinators are poorly documented. Similarly, we remain unsure of the effects on plant reproduction of population declines of other mammalian pollinators that are not yet listed as threatened or endangered species. Of particular concern is the plight of 17 primate species from Madagascar, Rwanda, Uganda, Zaire, and Comoro.

An endangered subspecies of lemur in Madagascar, the black-and-white ruffed lemur, is perhaps the only vertebrate with the agility and strength to open the floral bracts of *Ravenula madagascarensis* (known as the traveler's tree) to effect pollination (Kress et al. 1994). Its numbers have declined so precipitously that protection of its habitat is among the highest priorities for the Species Survival Commission of the World Conservation Union (IUCN) (Mittermeier et al. 1994). Other lemur species (e.g., *Daubentonia madagascariensis*) also access floral bracts and acquire pollen, but it is unknown whether they are a pollinator or a predator of the flowers (Mittermeier et al. 1994).

Well-documented case studies of non-flying mammal pollinators such as the black-and-white ruffed lemur are few, and substantial gaps remain in our understanding of the relative importance of nectar-feeding, non-flying mammals to the pollination of the plants they visit. Verifying successful pollination of canopy trees by mammals can be exceedingly difficult, and few species have been rigorously studied (Janson et al. 1981). Although the degree of rarity and rate of demographic declines are much better known for these mammals than for other taxonomic groups of pollinators, their pollination efficiency and specificity to particular plants are essentially unknown. In only a few cases has reduced seed set been documented where mammalian pollinator populations are limited (LaMont et al. 1993; Tepedino et al. 1996).

In reviewing the data on non-flying mammals as pollinators, we have identified the need for (1) field studies of IUCN-listed species of lemurs, monkeys, and other

nectar-feeders to determine how effective and specific they are as pollinators and which plants they pollinate; (2) evaluation of flowering trees visited by rare nectar-feeding mammals with respect to the availability of other surrogate or alternative pollinators, particularly on islands or highly fragmented mainland habitats (LaMont et al. 1993; Montalvo et al. 1997).

Hummingbirds and their Ecological Equivalents

Bird pollination is essential to the reproduction and survival of many plant species, as demonstrated by the relationship between Hawaiian honey creepers and endemic Hawaiian plants. In tropical and subtropical habitats of the New World, a substantial proportion of plants may rely on hummingbirds for pollination (Feinsinger 1987). Unfortunately, due to habitat destruction, avian malaria, and other influences, many of these plants and their specialist bird pollinators have become locally extirpated or threatened. Currently, at least 26 species of hummingbirds are sufficiently threatened to be of global conservation concern (Nabhan 1996). Their Old World analogs, the sunbirds, include at least another 7 species at risk. Other Australian, Indonesian, Micronesian, and Polynesian hovering birds are also at risk. Some forces behind these population declines include the destruction of habitats and the disruption of trap-lines and nectar corridors (Janzen 1974).

Although avian demographic studies are generally more available than those for bats, primates, marsupials, or invertebrates, we still lack such studies for most hummingbird and sunbird species. Hummingbird scarcity does not necessarily cause reproductive failure in plants they serve (Waser 1979; Linhart & Feinsinger 1980; Feinsinger et al. 1987). But declines in fruit set on a few plant species resulting from the temporal paucity of hummingbirds have been documented, even in places where carpenter bees and other animals may play a significant role in pollinating the same species (Waser 1979). We are unaware of any hummingbird or sunbird species that is the obligate pollinator of a particular plant, but it is likely that these birds play an important role in ensuring "ecological redundancy" (Aizen & Feinsinger 1994).

To better assess potential impacts of hummingbird declines, we need to (1) support training for a larger number of scientists to monitor and band hummingbirds and record their floral resources during migration; (2) determine the minimum levels of trap-line cohesiveness (for residents) and nectar corridor continuity (for migrants) required to maintain hummingbird movements, behaviors, and population levels; (3) develop a centralized database for banding and recapture of migratory hummingbirds and other avian pollinators, including a larger sample number of individuals and species to ascertain their migratory corridors; (4) determine the impact of the decline of "legitimate" pollinators on "cheaters" and

"robbers" visiting the same floral resources, and routinely take pollen samples from mist-netted birds visiting these flowers; and (5) carefully monitor fruit set where avian population changes are dramatic.

Perching Birds and Parrots

Although most pollination biologists have focused on nectar specialists like hummingbirds, honey creepers, or sunbirds, it should be noted that finches, vireos, white-eyes, and other similar birds often play important roles as secondary pollinators of many flowering plants. We lack confidence in the adequacy of studies assessing the importance of perching birds as pollinators relative to other floral visitors to the same plants. Certain plants, however, depend exclusively on perching birds for cross-pollination (Ford & Paton 1985). Lorikeets (parrots) are nonpasserine birds that often play a role in pollination. Over 70 species of passerine birds implicated as pollinators are also listed by the IUCN as threatened, endangered, or probably extinct (Nabhan 1996). The principal causes of endangerment include habitat destruction, conversion, and fragmentation; chemical fragmentation and pesticide exposure; hunting; and the introduction of exotic plants and birds that have disrupted native plant-pollinator relationships.

The most problematic gap in our knowledge is determining which passerine birds serve as legitimate agents of cross-pollination. Until avian ecologists apply refined methodologies to evaluate the pollination efficacy of various passerines, our information will remain incomplete.

To fill information gaps and better manage these avian pollinators, we have identified the need for (1) a symposium or research synthesis on passerines as pollinators to refine and standardize methodologies and to determine which behavioral and morphological traits predispose passerines to legitimate pollination; (2) verification of the presumed endangered status of passerine pollinators, matched with efforts to determine and reduce the pressures leading to their endangerment; and (3) maps of nectar corridors of migratory passerines and assessment of the degree to which areas for potential wildlife refuges along these corridors could be delineated.

Plants

The IUCN predicts a global loss of 20,000 flowering plant species within the next few decades; this will undoubtedly lead to the decline of the co-dependent pollinators who need them for survival (Heywood 1995). Pollinators that specialize on particular plant taxa, such as orchids, are more likely to be at risk than are "generalist" pollinators, or plant species that have multiple effective pollinators. In some cases, the loss of specialized pollinators will strongly select for self-compatibility, self-

pollination, and reduced genetic variability in plants, resulting in a possible reduction in their evolutionary adaptability to environmental change.

Populations of many native plants and their pollinators are being diminished and lost due to habitat fragmentation, degradation, and loss (LaMont et al. 1993; Kearns & Inouye 1997). Chemical habitat fragmentation due to the use of herbicides to keep deforested patches open can often aggravate physical fragmentation (Nabhan & Buchmann 1996). Further, both kinds of habitat fragmentation will accelerate the extirpation rate of local plant populations through inbreeding, genetic drift, and stochastic processes (Rathcke & Jules 1993).

More research needs to be pursued on habitat alterations that may be leading to a loss of biodiversity, initially of pollinators and followed soon thereafter by a decline in flowering plant diversity. Burd's (1994) evaluation of all available published case studies of reproductive shortfalls in flowering plants suggested that 62% of the species definitively studied are pollen-limited, although the magnitude of this estimate remains controversial. Other studies have found that pollinator limitation can reduce seed output by 50–60% in rare plants or plants in fragmented landscapes (Jennersten 1988; Pavlik et al. 1993; Bond 1995). Although some definitive work on global trends in plant extinctions has been done (Koopowitz et al. 1994), we need more information directly applicable to specific biomes to determine the magnitude of diminished pollinator populations or disrupted pollination processes on these vegetation types. This information is needed before important generalizations or discernible patterns that affect remedial techniques can be recognized.

To understand the magnitude of the effects of diminished pollinator populations and plant declines on ecological processes, we need to (1) allocate more resources to determine the extent to which extensive pollinator limitation is a natural occurrence in the plant world and to what extent it is aggravated by anthropogenic effects; (2) determine the relative degrees of pollinator limitation in fragmented or isolated populations versus more cohesive or widespread "core" populations; (3) determine the relative importance to plant reproductive success of pollinator limitation versus within-plant resource and genetic limitations; (4) establish monitoring programs to collect information on pollination, seed set, dispersal, and demographics for federal- and state-listed plants and those plant species listed by the Convention on International Trade in Endangered Species (Pavlik 1994; Falk et al. 1996); (5) determine critical habitat needs for federally listed plant species, with specific instructions for examining and including the habitats needed for supporting pollinators and seed dispersers when these may be limiting factors in the survival of listed species; (6) establish a category of environmental protection for threatened ecological relationships similar to those legislated for endangered species and de-

velop recovery plans accordingly; (7) underscore the importance of plant-pollinator relationships in educational media such as textbooks on ecology and conservation biology, elementary, secondary and college curricula, children's books, botanical gardens, natural history museums, and interpretive materials for parks and natural areas.

Consequences

Community Level

The ecological importance of pollinators in their communities is critical—perhaps outweighing the amount of attention formerly given them in studies of species diversity, population size, or biomass (Roubik 1993). If keystone plant species such as figs or dipterocarps lose their pollinators, for example, the entire structure of biotic communities will be dramatically changed (Kearns & Inouye 1997). In the case of tropical communities dominated by figs, 80% of the vertebrate species depend on figs as the basis of their diet (Bronstein et al. 1990). On oceanic islands with depauperate pollinator faunas, the loss of a single pollinator may result in a significant degradation of biodiversity. This is particularly true in the Southwest Pacific, where extirpation of flying fox populations will likely lead to cascades of linked extinctions in the island communities (Cox et al. 1991).

In one well-documented case, pesticide impacts on pollinators led to reductions in blueberry yields, which then affected a variety of organisms ranging from small birds and bears to human beings (Kevan 1977). These effects can be generated over tens of thousands of hectares as a result of imprudent insecticide spraying or fire suppression and can affect human activities such as crop production and the wild-plant harvesting traditions of indigenous peoples (Peigler 1994; Nabhan & Buchmann 1996). Even when linked extinctions are not documented, adverse impacts from wide-scale loss of pollinators can ripple through natural and human communities. Researchers should follow up on unverified reports of the adverse effects of pollinator loss in the "Brazil nut" industry of Brazil and Bolivia, where total fruit set failure has occurred in fragmented populations (Mori 1992). As discussed before, there are few studies that quantify the contributions of wildland pollinators to agricultural production. Reduction of pollinator faunas may translate directly into reduced prospects for developing "alternative pollinators," especially those recruited from wildlands immediately adjacent to farmlands.

Loss of pollinators from a biotic community may not be easily reversible. We do not know the time scale or magnitude of natural recolonization, how to remedy the loss of native pollinators, or even if such remedies are possible. The impacts of pollinator loss may extend to birds, spiders, lizards, and other predators of pollinating

animals. Protected areas are not always of sufficient size to ensure the maintenance of plant-pollinator relationships over time (Suzan et al. 1994). Pollinator breeding habitats and roosting and nesting sites may be different from their foraging sites; all must be considered in preserve establishment. The effects of external threats (emanating from beyond reserve boundaries) on pollinators must be considered in the design of biological preserves. Chemical fragmentation can exacerbate the effects of physical habitat fragmentation and is also of concern at the community level even where native vegetation appears intact (Nabhan & Buchmann 1996). Together, these forces may result in large-scale impacts on pollinator faunas. Introduction of exotic species such as predators and parasites may also have large negative impacts on pollinators.

Except for recent pollinator extirpations on oceanic islands (Cox et al. 1991), such ecological impacts are currently poorly understood. In addition there are substantial information gaps limiting our understanding of the persistence of pesticide residues in nectar-feeding organisms (Kearns & Inouye 1997). We are also concerned that pollinator-mediated hybridization between genetically engineered crops and cultivated or noncultivated relatives may occur at higher rates in fragmented habitats, with severe ecological and economic consequences (Ellstrand & Hoffman 1990).

Regional-scale effects are also of concern. Protected areas along migratory routes are critical to ensuring safe passage and sustenance of such migratory pollinators as monarch butterflies, nectar-feeding bats, and certain hummingbirds. The existing studies are highly indicative of negative consequences, but we need much more information to assess the magnitude of this problem. Because few scientists are trained to assess interactions between widely different species over large geographic ranges, we lack a large corpus of definitive studies.

Notwithstanding the recent contributions by Bronstein (1994), methodologies remain inadequate to integrate pollinator surveys at the community or landscape level, particularly in invertebrate taxonomy and plant systematics. More information is needed on carrying capacity estimates for pollinators, not only in terms of minimum plant population requirements and floral rewards per unit area, but also the required number of "safe sites" for roosting or nesting. The recent study of carrying capacity for long-nosed bats in Curacao is exemplary of what is needed (Petit & Pors 1996).

In general, we have identified the need for (1) recognition that pollination biology is not a narrow subdiscipline and that increased emphasis must be placed on pollination in the training of community ecologists, botanists, entomologists, and resource managers (Kearns & Inouye 1997); (2) a better focus at primary, secondary, and higher education levels on how pollination services benefit society; (3) the refining of pesticide impact stud-

ies on pollinator faunas, especially to include consideration of setbacks from habitats of pollinators; (4) identification and protection of major "nectar corridors" for migration paths of pollinators; and (5) encouragement of land managers of railroad and highway rights-of-way, golf courses, arboreta, and community and private gardens to plant appropriate native wildflowers that can sustain pollinators.

Consequences of Declines of Food Stability

In certain localities and some years, crop yield reductions have occurred due to pollinator scarcity in combination with other factors. Crop failures coincident with cold winter weather or drought may in fact be a function of adverse weather effects on pollinators. A yield decline in California almond orchards in 1995 can be attributed to a combination of weather and pollinator loss. In New Brunswick pesticide use and the resultant destruction of pollinators caused a multi-million dollar loss in the blueberry crop (Kevan 1977). In 1996 in Ontario, cherry prices rose due to a combination of bad weather and the presence of mites that parasitized honey bee pollinators. Historically, alfalfa seed crop losses have been attributable to pollinator loss (Stephen 1959). More recently, pumpkin crops in New York have declined for this reason (Watanabe 1994). Cashew nut crop failures in north Borneo have occurred because this nut species was moved from its native habitat (Brazil) to the Old World tropics, without a native pollinator becoming available. Pollinator losses may effect not only total harvest but harvest quality. Some crops that have been harvested show evidence (e.g., misshapen or small fruit) of pollinator failure.

Current biological knowledge pertinent to economic modeling is inadequate to reconstruct total economic losses in agriculture from the loss of pollinators. The economic burden of reduced yields and crop production cost increases resulting from honey bee declines alone has been estimated at \$5.7 billion a year (Southwick & Southwick 1992). Although we suspect losses to be at least this substantial, more data are needed to quantify the magnitude of the damage. We need a better understanding of the relationships among pollinator diversity, pollinator abundance, and changes in crop yields. We are concerned that few studies have followed the chain from pollinator foraging to crop harvest. We have relied entirely too much on a single introduced generalist pollinator, the European honey bee, to carry out the bulk of agricultural pollination. Even so, there are no U.S. statistics on how much of a role biology, weather, and the cessation of honey price support programs has each played in the decline of managed honey bee colonies since 1986.

For many crops we do not know the complete cast of floral visitors, or, when we do, we do not know how ef-

ficient these floral visitors are. We need careful analyses of how efficient and reliable different floral visitors are in accomplishing pollination and cross fertilization. We also lack basic knowledge of plant reproductive biology for most common crop plants. In particular, there is a paucity of literature dealing with the nectar and pollen availability of newer cultivars, which may differ from older heirloom crop varieties. We need better understanding of the ways in which floral traits shape the efficiency of pollination and how to translate them into improved crop harvests and enhanced agronomic quality. Even crops that may not require pollination for fiber or vegetable harvests may require pollination to produce the seed crop. Some crops that do not require pollination, such as cotton, can nevertheless produce improved yields and quality when pollinated (Pimentel et al. 1992). We are certain that variance in annual yields of crops will increase if pollination continues to be perceived as a "free service" and if no action is taken to halt population declines and protect pollinators.

With regard to pollination services and food yield stability, we need to (1) invest in the development or domestication of (non-*Apis*) alternative pollinators that can be employed when the services provided by managed honey bees are inadequate to ensure high fruit set (Batra 1996); (2) discern the reproduction-limiting factors for cultivated plants, particularly for poorly studied specialty crops, and determine which insect visitors to these crops will increase pollination rates; (3) determine the degree to which intercropping, hedgerows, and other farm management practices can maintain pollinators by providing increased nesting or foraging sites; (4) encourage modern crop breeders to consider the floral attributes of interest to pollinators—color, scent, amount of nectar and pollen, self-incompatibility, and floral morphology—when selecting new horticultural varieties; and (5) preserve genetic stocks of honey bees as well as those of alternative managed pollinators.

Literature Cited

- Aizen, M. A., and P. Feinsinger. 1994. Habitat fragmentation, pollination, and plant reproduction in a Chaco Dry Forest, Argentina. *Ecology* **75**:330–351.
- Batra, S. 1996. Unsung heroes of pollination. *Natural History* **106**(4): 42–43.
- Bond, W. J. 1995. Assessing the risk of plant extinction due to pollinator and disperser failure. Pages 122–128 in J. G. Lawton and R. M. May, editors. *Extinction rates*. Oxford University Press, Oxford, United Kingdom.
- Bronstein, J. L. 1994. The plant-pollinator landscape. Pages 256–288 in L. Hansson, I. Fahrig, and G. Merriam, editors. *Mosaic landscapes and ecological processes*. Chapman and Hall, London.
- Bronstein, J. L., P. H. Gouyon, C. Gliddon, F. Kjellberg, and G. Michaloud. 1990. The ecological consequences of flowering asynchrony in monoecious figs: a simulation study. *Ecology* **71**:2145–2156.
- Buchmann, S. L. 1996. Competition between honey bees and native bees in the Sonoran Desert and global bee conservation issues. Pages 125–142 in A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich, and I. H. Williams, editors. *The conservation of bees*. Academic Press, Harcourt Brace, London.
- Buchmann, S. L., and G. P. Nabhan. 1996. *The forgotten pollinators*. Island Press, Washington, D.C.
- Burd, M. 1994. Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. *Botanical Review* **60**:81–109.
- Clark, D. R., Jr. 1981. Bats and environmental contaminants: a review. Special scientific report no 235. U.S. Fish and Wildlife Service, Washington, D.C.
- Cox, P. A., T. Elmquist, E. D. Pierson, and W. E. Rainey. 1991. Flying foxes as strong interactors in South Pacific island ecosystems: a conservation hypothesis. *Conservation Biology* **5**:448–453.
- Ellstrand, N. C., and C. A. Hoffman. 1990. Hybridization as an avenue of escape for engineered genes. *BioScience* **40**:438–442.
- Falk, D. A., C. I. Millar, and M. Olwell. 1996. *Restoring diversity: strategies of reintroduction of endangered plants*. Island Press, Washington, D.C.
- Federal Register. 1988. Listing criteria for bats. U.S. Office of Endangered Species, Fish and Wildlife Service, Washington, D.C.
- Feinsinger, P. 1987. Approaches to nectarivore-plant interactions in the New World. *Revista Chilena de Historia Natural* **60**:285–319.
- Feinsinger, P., J. H. Beach, Y. B. Linhart, W. K. Busby, and K. G. Murray. 1987. Disturbance, pollinator predictability, and pollination success among Costa Rican cloud forest plants. *Ecology* **68**:1294–1305.
- Fleming, T. H. 1993. Plant-visiting bats. *American Scientist* **81**:460–467.
- Ford, H. A., and D. C. Paton. 1985. *The dynamic partnership: birds and plants in southern Australia*. D. J. Woolman, Government Printer, South Australia.
- Free, J. B. 1993. *Insect pollination of crops*. Academic Press Limited, London.
- Fujita, M. S. 1991. Flying fox (*Chiroptera:Pteropididae*) pollination, seed dispersal, and economic importance. Resource publication 2. Bat Conservation International, Austin, Texas.
- Heywood, V. H., editor. 1995. *Global biodiversity assessment*. UNEP/Cambridge University Press, Cambridge, Massachusetts.
- Ingram, M. 1996. Ten essential reasons to protect the birds and the bees: how an impending pollination crisis threatens plants and the food on your table. *Forgotten pollinators campaign*, Arizona-Sonora Desert Museum, Tucson.
- Janson, C. H., J. Terborgh, and L. H. Emmons. 1981. Non-flying mammals as pollinating agents in the Amazonian forest. *Biotropica* **13**: 131–136.
- Janzen, D. H. 1974. The de-flowering of Central America. *Natural History* **83**:49.
- Jennersten, O. 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. *Conservation Biology* **2**:359–366.
- Kearns, C. A., and D. W. Inouye. 1997. Pollinators, flowering plants, and conservation biology. *BioScience* **47**:297–307.
- Kevan, P. G. 1977. Blueberry crops in Nova Scotia and New Brunswick: pesticides and crop reductions. *Canadian Journal of Agricultural Economics* **25**(1):64.
- Koopman, K. F. 1981. The distribution of New World nectar-feeding bats. *Annals of the Missouri Botanical Garden* **68**:352–369.
- Koopowitz, H., A. Thornhill, and M. Anderson. 1994. A general stochastic model for the prediction of biodiversity losses based on habitat conversion. *Conservation Biology* **8**:425–438.
- Kress, W. J., G. E. Schatz, M. Andrianifahanana, and H. S. Morland. 1994. Pollination of *Ravenala madagascariensis* (Strelitziaceae) by lemurs in Madagascar: evidence for an archaic pollination system? *American Journal of Botany* **81**:542–551.
- LaMont, B. B., P. G. L. Klinkhamer, and E. T. F. Witkowski. 1993. Population fragmentation may reduce fertility to zero in *Banksia goodii*: a demonstration of the Allee effect. *Oecologia* **94**:446–450.
- Linhart, Y. B., and P. Feinsinger. 1980. Plant-hummingbird interac-

- tions: effects of island size and degree of specialization on pollination. *Journal of Ecology* **68**:745-760.
- Loper, G. M. 1995. A documented loss of feral honey bees due to mite infestations in southern Arizona. *American Bee Journal* **December**: 823.
- Matheson, A., S. L. Buchmann, C. O'Toole, P. Westrich, and I. H. Williams, editors. 1996. *The conservation of bees*. Academic Press, Harcourt Brace, London.
- McGregor, S. E., S. M. Alcorn, and G. Olin. 1962. Pollination and pollinating agents of the Saguaro. *Ecology* **43**:259-267.
- Mickleburgh, S. P., A. M. Hutson, and P. A. Racey. 1992. Old World fruit bats: action plan for their conservation. IUCN-SSC Chiroptera Specialist Group, World Conservation Union, Gland, Switzerland.
- Mittermeier, R. A., I. Tattersall, W. R. Konstant, D. M. Meyers, and R. B. Mast. 1994. *Lemurs of Madagascar*. Conservation International, Washington, D.C.
- Montalvo, A. M., S. L. Williams, K. J. Rice, S. L. Buchmann, C. Cory, S. N. Handel, G. P. Nabhan, R. Primack, and R. H. Robichaux. 1997. Restoration biology: a population biology perspective. *Restoration Ecology* **5**:1-14.
- Mori, S. 1992. The brazil nut industry: past, present, and future. Pages 241-251 in M. Plotkin and L. Famolare, editors. *Sustainable harvesting and marketing of rain forest products*. Island Press, Washington, D.C.
- Nabhan, G. P. 1996. Global list of threatened vertebrate wildlife species serving as pollinators for crops and wild plants. Forgotten Pollinators Campaign, Arizona-Sonora Desert Museum, Tucson.
- Nabhan, G. P., and S. L. Buchmann. 1996. Pesticide disruption of interactions between rare plants and their pollinators: chemically-induced habitat fragmentation in the U.S./Mexico borderlands? *Comments in Toxicology* **5**:475-486.
- Nabhan, G. P., and S. L. Buchmann. 1997. Services provided by pollinators. Pages 133-150 in G. Daily, editor. *Nature's services*. Island Press, Washington, D.C.
- National Agricultural Statistics Service. 1997. 1996 honey production report. U. S. Department of Agriculture, Washington, D.C.
- O'Toole, C. 1993. Diversity of native bees in agroecosystems. Pages 169-196 in J. LaSalle and I. D. Gauld, editors. *Hymenoptera and biodiversity*. Center for Agriculture and Biosciences (CAB) International, Wallingford, England.
- Pavlik, B. M. 1994. Demographic monitoring and the recovery of endangered plants. In M. L. Bowles and C. G. Whelan, editors. *Restoration of endangered species*. Cambridge University Press, Cambridge, Massachusetts.
- Pavlik, B. M., N. Ferguson, and M. Nelson. 1993. Assessing limitations on the growth of endangered plant populations. II. Seed production and seed bank dynamics of *Erysimum capitatum* ssp. *angustatum* and *Oenothera deltooides* ssp. *bowellii*. *Biological Conservation* **65**:267-278.
- Peigler, R. S. 1994. Non-sericultural uses of moth cocoons in diverse cultures. *Proceedings of the Denver Museum of Natural History Series* **3(5)**:1-20.
- Petit, S., and L. Pors. 1996. Survey of columnar cacti and carrying capacity for nectar-feeding bats on Curacao. *Conservation Biology* **10**:769-775.
- Pimentel, D., H. Acquay, M. Biltonen, P. Rice, M. Silva, J. Nelson, V. Lipner, S. Giordano, A. Horowitz, and M. D'Amore. 1992. Environmental and economic costs of pesticide use. *BioScience* **42**:750-760.
- Rathcke, B. J., and E. Jules. 1993. Habitat fragmentation and plant/pollinator interactions. *Current Science* **65**:273-278.
- Roubik, D. W. 1993. Direct costs of forest reproduction, bee-cycling, and the efficiency of pollination needs. *BioScience* **18**:537-552.
- Roubik, D. W. 1995. Pollination of cultivated plants in the tropics. *Agricultural services bulletin* 118. Food and Agriculture Organization, Rome, Italy.
- Southwick, E. E., and L. Southwick, Jr. 1992. Estimating the economic value of honey bees (*Hymenoptera Apidae*) as agricultural pollinators in the United States. *Economic Entomology* **85**:621-633.
- Stephen, W. P. 1959. Maintaining alkali bees for alfalfa seed production. Page 123 in *Bulletin* 568. Oregon Agricultural Experiment Station, Corvallis, Oregon.
- Sutton, R. H., and P. D. Wilson. 1983. Lead poisoning in grey-headed fruit bats (*Pteropus poliocephalus*). *Journal of Wildlife Diseases* **19**:294-296.
- Suzan, H., G. P. Nabhan, and D. T. Patten. 1994. Nurse plant ecology and floral biology of a rare, night-blooming cactus, (*Peniocereus striatus* (Brandegee)) Buxbaum. *Conservation Biology* **8**:461-470.
- Tepedino, V., R. Levin, J. Donovan, and G. P. Nabhan. 1996. Monitoring and assessing threats to rare and endangered plants, their pollinators and habitats. Forgotten Pollinators Campaign, Arizona-Sonora Desert Museum, Tucson.
- U.S. Fish and Wildlife Service. 1994. Mexican long-nosed bat (*Leptonycteris nivalis*) recovery plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico.
- Valiente-Banuet, A., M. D. C. Arizmendi, A. Rojas-Martinez, and L. Dominguez-Canseco. 1995. Ecological relationships between columnar cacti and nectar-feeding bats in Mexico. *Journal of Tropical Ecology* **12**:103-119.
- Waser, N. M. 1979. Pollinator availability as a determinant of flowering time in ocotillo (*Fouquieria splendens*). *Oecologia* **39**:107-121.
- Washitani, I. 1996. Predicted genetic consequences of strong fertility selection due to pollinator loss in an isolated population of *Primula seiboldii*. *Conservation Biology* **10**:59-64.
- Watanabe, M. 1994. Pollination worries rise as honey bees decline. *Science* **265**:1170.