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Synthesis, part of Special Feature on [Pollinator Decline](#)

North American Dipteran Pollinators: Assessing Their Value and Conservation Status

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ABSTRACT

Recent attention to pollinator declines has focused largely on bees and vertebrates. However, few pollination systems are obligate, and pollinators that complement the role of bees may respond differently to environmental disturbance. The conservation status of North American fly pollinators remains undocumented. In this paper, methods for monitoring shifts in dipteran pollinator abundance are discussed. The need for further basic research into pollination by flies is addressed, and the significance of dipteran conservation is considered.

KEY WORDS: anthophilous flies, anthropogenic disturbance, conservation, Diptera, Dipteran conservation, generalist pollinators, North America, pollination, pollinator declines, population fluctuation, redundant pollination systems.

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INTRODUCTION

Anthropogenic disruption of pollination systems will likely pose consequences to plant and pollinator diversity, and to linked organisms within communities (Kearns et al. 1998). Although attention is often focused on bees and vertebrate pollinators (Williams 1986, Gauld et al. 1990, Torchio 1990, Day 1991, Osborne et al. 1991, La Salle and Gauld 1993, Batra 1995, Buchmann and Nabhan 1996, Matheson et al. 1996, Watanabe 1994; [Migratory pollinators and their corridors](#)), other groups of insect pollinators play roles that are not thoroughly understood. Few pollination systems are obligate, and pollinators that complement the role of bees may respond differently to environmental disturbance. The value of North American fly pollinators is not thoroughly understood, and concerns relating to pollinator declines in North America have not extended to dipteran pollinators. In this paper, methods for monitoring shifts in dipteran pollinator abundance are discussed. The need for further basic research into fly pollination is addressed, and the significance of dipteran conservation is considered.

REPORT

Diptera as pollinators

Dipterans are among the most common insects that visit flowers. At least 71 dipteran families contain anthophilous species (Larson et al. 2001). Flies have been mentioned as pollinators or regular visitors of at least 555 species of flowering plant (Larson et al. 2001) and pollinators of over 100 cultivated plants including cacao, mango, cashew, tea, and onions (B. M. H. Larson, D. W. Inouye, and P. G. Kevan, *unpublished manuscript*). Many families of North American flies contain pollinators. Some of the larger, more notable pollinating flies belong to the families Bombyliidae, Syrphidae, Anthomyiidae, Tachinidae, Calliphoridae, and Muscidae. Small nematoceran fly pollinators include, but are not restricted to, the Bibionidae, Chironomidae, Culicidae, Empididae, Mycetophilidae, and Cecidomyiidae (Kevan and Baker 1983).

Anthophilous flies are diverse, ranging from opportunistic nectar and pollen consumers to specialized nectarivores. Fly proboscides range from a few millimeters up to 70 mm in length in a South African nectarivorous, nemestrinid fly (Manning and Goldblatt 1995). In a distinct syndrome called sapromyophily, certain flies (e.g., Calliphoridae) are deceived into pollinating flowers that produce odors of decay and mimic the decaying flesh in which these flies normally oviposit. The diversity of forms of flower-visiting flies is great; consequently, flies vary significantly in the amount of pollen that they carry, in the time that they spend in flowers, and in their effectiveness as pollinators (B. M. H. Larson, D. W. Inouye, and P. G. Kevan, *unpublished manuscript*).

Some of the many anthophilous fly species in North America have been assessed for their value as pollinators (e.g., Nye and Anderson 1974, Burgett 1980, Mesler et al. 1980, Levesque and Burger 1982, Boyle and Philogène 1983, Campbell and Motten 1985, Motten 1986, Kearns and Inouye 1994, Jarlan et al. 1997*a, b*). A recent review (B. M. H. Larson, D. W. Inouye, and P. G. Kevan, *unpublished manuscript*) that details the pollen-carrying abilities, constancy, and effectiveness of fly pollinators indicates that flies may contribute significantly to the pollination of North American flowers. Even flies that are generalists in their floral visits can contribute to plant reproductive success, and may equal or rival bees as effective pollinators in some circumstances (Motten 1986, McGuire and Armbruster 1991, Kearns and Inouye 1994). The predominance of flies on certain arctic and alpine flowers makes their contributions particularly important in these environments (Downes 1965, Hocking 1968, Mani 1968, Kevan 1972, Pojar 1974, Arroyo et al. 1982, 1985, Primack 1983, Shaw and Taylor 1986, Inouye and Pyke 1988, Kearns and Inouye 1994, Elberling and Olesen 1999). Much remains to be learned about the importance of fly pollination in other habitats. In addition, our understanding of the contributions of fly pollinators is poor for those flowers that attract multiple insect species whose numbers fluctuate independently.

Most entomophilous flowers receive visits from several different types of insects (Moldenke 1976, Herrera 1988, Ellis and Ellis-Adams 1993, Petanidou and Ellis 1993, Waser et al. 1996). For example, in a study of 2200 plant species in California, 71% of the outcrossing species were visited by two potential pollinators and 49% were

visited by three or more potential pollinators (Moldenke 1976); 91% of 666 phrygana plant species in a botanical reserve in Greece were visited by five or more insect species (Petanidou and Ellis 1993). Redundancy in pollination systems is probably the rule, rather than the exception. Many species of flies are generalists that visit multiple plant species (D. W. Inouye, *unpublished data*) and their contributions to plant reproductive success are likely to be discounted because of their reputation as ineffective pollinators (Faegri and van der Pijl 1979, Richards 1986). However, the complexity of interactions in redundant pollination systems deserves further attention. When multiple pollinator species visit the same flowers, their respective value as pollinators is interdependent (Thomson and Thomson 1992), and may differ from year-to-year or even over the course of the flowering season. An inefficient, but legitimate, pollinator could remove pollen from the system (e.g., by eating it or carrying it to flowers of a different species) and prevent an efficient pollinator from delivering that same pollen to a conspecific flower. The same inefficient pollinator may be of great value to the plant's reproductive success when the more efficient pollinator is absent (Kearns and Inouye 1994). Petanidou and Ellis (1993) suggest that the presence of multiple pollinating species creates "a regime of selective noise" that could halt floral evolution. Redundant pollination systems and the role of flies in these systems deserve further attention.

Dipteran pollinator declines: is there evidence?

Diptera tend to be small, noncharismatic, and difficult to identify. The basic biology of most species is poorly understood. These factors are likely to be responsible for the minimal conservation focus on the order. Insect conservation efforts have tended to focus on large and showy species, particularly butterflies and dragonflies (Samways 1994). As early as 1835, the Apollo butterfly (*Parnassius apollo*) was granted legislative protection in Bavaria. Since that time, several conservation organizations have focused attention on butterflies and, more recently, on other insect groups. For example, the IUCN (International Union for the Conservation of Nature) now has Specialist Groups on social insects, Lepidoptera, Odonata, Orthopteroidea, and water beetles (Samways 1994).

There is no documented evidence of recent declines of North American fly pollinators. However, I am not aware of any studies that have specifically addressed this issue. Only one fly is listed as endangered on the U.S. Fish and Wildlife Service endangered species list ([US Listed Insect Species Profiles](#)), and that is a nectarivorous fly, *Rhaphiomidas terminatus abdominalis* (Apioceridae). That only one dipteran is listed is not likely to be indicative of the actual number that are rare, endangered, or in decline, but perhaps is more indicative of our lack of knowledge in this area. Far more research on the importance of fly pollination, fly abundance, and community composition will be necessary to make any broad generalizations about the conservation status of fly pollinators in North America.

Several models for the types of studies necessary are available from research conducted in other parts of the world (e.g., Bañkowska 1980, 1981, Owen and Gilbert 1989, Inoué et al. 1990, Kakutani et al. 1990, Kato et al. 1990). A number of North American studies that were designed to address different issues can also provide useful information.

There are two important components to the issue of pollinator declines. One is an absolute change in abundance and the second is a change in species composition. Different sets of difficulties are associated with addressing each of these issues.

Dipteran abundance

Different species of insects in the same community can show independent fluctuation patterns ranging from small to extreme, making it difficult to ascribe a single environmental process to changes in abundance (Wolda 1992). The complex and varied life histories of flies may obscure patterns in fluctuations if one does not understand differences in the basic biology of different species. For example, larval habits of flies range from predatory through saprophytic and parasitic. When we are concerned with the abundance of anthophilous flies, we generally think of adult forms that feed at flowers. However, larval food supplies could be more important in producing differences in fluctuations among species (Bañkowska 1980). Different life styles, different larval habitats, and differences in the regional distribution (broad or restricted ranges) could also result in different patterns of population stability (Owen and Gilbert 1989). If larval food is a key resource for most fly species, fly species may show significantly different patterns of fluctuation than bees whose larvae are all dependent on pollen for food, reinforcing the idea that different pollinator groups may respond differently to environmental change.

Anthropogenic changes in fly species abundances may be difficult to monitor unless there are baseline data on

natural population fluctuations. Although measures of the abundances of mosquitoes, tsetse flies, or pest species receive much attention (Williams et al. 1990, [American Mosquito Control Association](#), [Integrated Satellite and Field Data Analysis of ODA and Other Tsetse and Trypanosomiasis Research and Control Programmes](#)), other types of flies are monitored less frequently. In North America, few extensive data sets exist that are specific to anthophilous flies. However, other types of studies, designed with different questions in mind, can be further analyzed to provide measure of relative abundance of anthophilous fly species. Three of these are discussed here to give the reader a sense of the types of studies that might be applicable.

In 1947, R. H. Whittaker (1952) conducted extensive sweep-net sampling of different insect communities in the Great Smoky Mountains of Tennessee and North Carolina. He sampled 16 sites, representing 13 distinct plant communities, and sorted insects to species. The 13 main sites were each sampled three times on different days in June and July of 1947. The vegetation within sites was divided into herb, shrub, and low-tree strata. Samples consisted of 50 successive sweeps within each stratum. Some supplementary collecting of large flying insects missed during sweep samples was performed. Over 8000 Diptera were collected, and the abundances of 45 families was presented for each site. Diptera ranged from 28% to 58% of the total sample per site. The scale of this survey was extensive; all but three of the sites were within the Great Smoky Mountains National Park and are likely to have had minimal impact compared to private lands studied over 50 years ago.

Another large-scale survey was conducted by Siemann et al. (1996; Long Term Ecological Research, University of Minnesota) in 1992 in Cedar Creek, Minnesota. Sweep samples of 48 grassland fields were conducted 7-9 times during the growing season, with 100 sweeps per sampling date. 89,596 insect specimens of 1167 species were collected, and 90% of the specimens were identified to species. The data set was used for analysis of diversity, abundance, and body size relationships of insects, but it might lend itself to reanalysis for patterns in anthophilous fly distribution. LTER sites could be targeted as locations for these types of surveys, to be repeated on a long-term basis.

In 1984, D. Inouye and M. Soulé initiated several long-term monitoring projects related to organisms occurring in the area of the Rocky Mountain Biological Laboratory (RMBL) in Colorado (latitude N 38.5°, 106° W). Malaise trapping has been continued since that time (D. W. Inouye, *unpublished data*). Samples were collected weekly throughout the growing season from June through late August at Gothic Research Meadow (elevation 2912 m). In 1991, trapping began at two additional sites in the area (Cement Creek, elevation 2830 m; and Washington Gulch, 2978 m). The malaise trap catches were sorted to insect order, and the numbers of flies in certain families of interest were recorded for each sample. Relative weather data were recorded for each 72-h collecting period, and could be supplemented by more detailed weather data from the RMBL weather station. The peak number of Diptera within each years' collections ranges from a low of 280 in 1995 to over 1665 individuals in 1985. Preserved specimens are in storage for future extended analysis.

Dipteran species composition

Differences in dipteran species composition between natural and disturbed areas can be dramatic, and can serve as excellent indicators of environmental degradation (Bańkowska 1980). In an extensive 5-yr survey of syrphid biogeography in Poland, Bańkowska (1980) compared the syrphid fauna of multiple natural areas with those from areas subjected to mild, moderate, and intensive anthropogenic pressures. She documented a lower species diversity in urban and agricultural areas. Both were dominated by syrphid species with broad distributional ranges, good colonizing abilities, and high ecological tolerances. In comparison, natural habitats were species-rich and characterized by shifting proportions of species, as one moved from one habitat toward another. There were characteristic species associations for each distinct habitat type. Syrphid fly species composition closely followed patterns of food supply and habitat condition.

The following example illustrates Bańkowska's findings: In total, 73 species were collected in the city of Warsaw, compared to 128 species in natural areas containing Warsaw's pre-urban habitat of oak-hornbeam forest. Only 66 species inhabited urban parks, and 46 species inhabited green areas around housing estates. The proportion of phytophagous and terrestrial saprophagous species dropped significantly, with only four species of phytophages present near the housing estates. These four were pests that eat ornamental plants, or weed-eating species. Urban areas were dominated by four syrphid species with broad geographic ranges

Clearly, this type of information on dipteran species composition will be invaluable in determining whether North American fly pollinators are in decline. Bańkowska's comparison of species composition in disturbed and natural

habitats is a good model for the type of study needed in North America. This type of study could be tied to a second project estimating the pollination value of different dipteran species.

In Japan, a broad-scale, four-year survey compared all insect visitors to roughly 100 plant species in each of three different habitats (Inoue et al. 1990, Kakutani et al. 1990, Kato et al. 1990). The habitats included a university campus with mostly exotic vegetation, an undisturbed oak forest, and a botanically rich mosaic containing both native deciduous and planted coniferous forest. This project involved the collection and identification of several thousands of flower-visiting insects or arachnids in each habitat. Information on flowering and insect phenology and plant breeding systems was collected as well. Again, the site of greatest human disturbance was poorest in species numbers (Kakutani et al. 1990). The total number of arthropod species collected on the plants of the university campus was 37% of the total of the oak forest and 23% of the total mosaic of natural and planted forest (Kakutani et al. 1990).

To look at anthropogenic effects on dipteran species composition, one can compare different sites as in the studies just described, or one can look within a site at how species composition changes over time with changes in habitat. The later type of study involves resampling historical data sets for the continued presence of species. If we attempt to use historical data sets, we need to remember that they may not represent complete lists of the species that were present. Resampling efforts may produce more or fewer species, depending upon the effort and techniques employed. Disney (1986) recounts a survey of insects conducted by the Yorkshire Naturalists' Union from 1954 to 1958, in which 436 species of Diptera were collected from the Malham Tarn in England (Flint 1963). Renewed attempts to produce a comprehensive list of Diptera in the 1970s resulted in a species list in excess of 1000. Disney attributes the increase in numbers to the use of multiple collecting methods, intensified efforts, and the availability of better keys for recognizing or separating species.

If we recognize the limitations of resampling, large collections from circumscribed locales can still provide useful data on the historical presence of dipteran species; these data can be compared with modern-day presence/absence data. Although presence/absence data are not quantitative, they can provide the same sort of information derived from Bañkowska's (1980) studies relating to the "weediness" of species that dominate disturbed habitats. Areas that have been extensively sampled in the past could be targeted as sites for renewed collecting activity. Large-scale data compilations of the insect visitors to the flora of a region, such as that compiled for northwestern Europe by Ellis and Ellis-Adams (1993), could also serve as baseline data. I will discuss two large-scale North American studies of historical value.

One collection that lends itself to resampling is the product of an anthophilous insect survey conducted by Charles Robertson at the turn of the last century (see [Marlin and LaBerge 2001](#)). Robertson collected and identified insects visiting flowers within 10 miles of Carlinville, Illinois, over the course of about 30 years (Robertson 1929). He examined 441 flowering plant species and identified 446 species of Diptera visiting flowers. Changes in land use have been documented for the area since the original collection.

A major study, initiated by Andrew Moldenke (1975, 1976; see also Moldenke and Neff 1974*a, b*), documented insect visitors to plants of 17 different habitats in California as part of a hemispheric attempt to compare equivalency of insect communities. Over eight years, 800,000 pollinators were recorded on 2200 plant species. Over 76,000 fly specimens were collected. Pollination studies of several hundred plants confirmed whether or not insects were true pollinators of these species. Moldenke determined the number of plant species used by each major category of pollinator within each habitat. Broad categories of flies included in the study were Bombyliidae, muscoid flies, and Syrphidae. Specimens that were collected were identified to species whenever possible. Resampling sites from this study for the current presence of species would provide significant information relating to changes in fly species diversity. This study also contains semiquantitative data, because all insects visiting flowers were collected during sampling periods. Moldenke stated that the relative abundance of species collected may not always reflect the true proportional representation, but he made corrections to help account for bias. Errors in representation stem from two sources: (1) the fact that the fastest and most wary species may be underrepresented. Attempts were made to correct for this problem by factoring in the success rate of capture. (2) The most common insect species are underrepresented because collectors key in on unusual and interesting specimens. Again, attempts were made to correct for this bias (Moldenke 1975). This enormous data base might serve as the basis for large-scale resampling efforts to assess the extent of change since the early 1970s.

Floral visitation studies

A number of floral visitation studies designed to address some aspect of floral biology or insect activity may also be useful in providing baseline data on species composition of dipteran visitors to specific plants (e.g., Boyle and Philogène 1983, Campbell and Motten 1985, Motten 1986, Shaw and Taylor 1986, McCall and Primack 1992).

Among visitation rate studies, site-to-site variation in fly numbers seems to be the norm (Toft 1983, Herrera 1988, Kearns and Inouye 1994). At one site, a particular fly may be the predominant pollinator, effecting high percentages of seed set, whereas in another plant population, that same species (or even the entire family of flies that it represents) is absent from the array of flower visitors (Mesler et al. 1980). Even within a single site, visitation rates can be affected not only by changes in fly abundance, but also changes in floral density, floral species available, and competition for nectar with other insects (Herrera 1988). On a shorter time scale, visitation rates are affected by temperature, wind, and light conditions (Primack 1978, Herrera 1988, McCall and Primack 1992). In general, studies that have looked at visitation patterns of pollinators over several years also note great variability among years (Herrera 1988, Schemske and Horvitz 1989, Kearns and Inouye 1994, Pellmyr and Thompson 1996).

When spatiotemporal variability is large, resampling will be difficult. However, broad patterns of change in the types of floral visitors, such as those detected by Bañkowska (1980), may be apparent in disrupted habitats. Resampling of habitats that have remained intact could be combined with sampling disturbed areas containing the same plant species.

To give the reader a sense of what sorts of studies exist and how variable the data can be, I mention a few of the North American studies of visitation rates that span more than one season, and that could be easily replicated. This is not meant to be a comprehensive list of replicable studies.

Boyle and Philogène (1983) studied the variations in abundance and significance of native pollinators in an apple orchard in Ontario for three years. Apple blossoms were monitored for insect visitors throughout the blooming period each year. Weather conditions and numbers of apple blossoms were also recorded. Insects collected were noted to species, but insects visiting flowers were grouped into 20 categories that included seven groups of flies. 11,401 insects were observed in the three-year survey.

McCall and Primack (1992) compared insect visitation patterns to flowers in three different communities. Two of the three study sites were in North America: tundra habitat of White Mountain National Forest, New Hampshire at two different elevations (46° 16'N, 71° 18'W; 1664 m and 1539 m; 320 observation periods; 35 plant species; three growing seasons); Rock Meadow Conservation Area, Belmont, Massachusetts (42° 23'N; 71° 23'W; 2 years; 649 observation periods in 1982; 124 plant species, 392 observation periods in 1983, 108 plant species). Visitation was measured using the standardized 10-min visitation periods introduced by Arroyo et al. (1982). They counted any insects touching reproductive parts of flowers, and classified them to order in the field. Representative specimens were archived at Boston University. Plant species were observed in proportion to their abundance in the habitat. Flies made roughly 10% of the visits to flowers at the woodland site, and over 90% of the visits at the tundra site.

Catherine Reed (1995a, b) monitored species richness of insects on prairie flowers in southeastern Minnesota for three years. She worked in eight separate prairie remnants or prairie reconstruction sites, hand-collecting all insects during 15-min sampling sessions on each plant species that had at least 100 open flowers (59 plant species). The focus of the study was to compare diversity in reconstructed sites with diversity in remnant prairie patches. Collections were made from late May through late September on sunny days when temperatures were between 20° and 35°C. Insects were identified to species. Sixty fly species were collected, some in reconstructions, others in remnants, some in both. Reed revisited the sites in the summer of 1999, and says the study is "quite repeatable," although some of the sites have changed. Native prairie sites are now managed more intensely with brush-cutting, burning, and planting of seeds (C. Reed, *personal communication*).

Kearns (1990) and Kearns and Inouye (1994) monitored visitation rates to *Linum lewisii* (Linaceae) for three summers at three different elevations in the area of Rocky Mountain Biological Laboratory, Gothic, Colorado (38.5° N, 106.5° W; 2780 m, 2886 m, and 3475 m). Visitation data were recorded for bees and fly families. Fly visitation rates differed significantly among sites, but did not differ significantly among years. However, additional visitation data collected at the 2886m site in the two preceding years showed that annual variation in visitation within a site can be large, in this case, as a result of an *Entomophora* outbreak in 1986 that reduced fly numbers. Visitation rates to *Linum* are highly correlated with Malaise trap fly samples from the same site (Kearns and

Inouye 1994).

DISCUSSION

An attempt to document the conservation status of fly pollinators in North America reveals the need for further basic research into fly pollination systems, and into the natural fluctuations in dipteran abundance. The main impediment to implementing any of the large-scale studies recommended is that intensive collecting efforts produce large numbers of species that require identification. Fly species identifications are often difficult, and the number of fly taxonomists is limited. Revisions in taxonomy of certain groups may mean re-evaluating original sample material from historical collections. These problems are not unique to Diptera, but are common to any large-scale insect collections.

The abundance and diversity of anthophilous flies, their role in pollination systems, and their multiplicity of larval roles indicate that dipteran declines would probably affect multiple levels within communities. The development of checklists for specific areas (e.g., Biosphere Reserves or National Parks) would be a useful first effort (Disney 1986). Resampling in areas of well-documented studies would provide much needed data that would allow us to evaluate the conservation status of the group. Habitat conservation will ultimately be the most effective tool in conserving pollinating Diptera.

RESPONSES TO THIS ARTICLE

Responses to this article are invited. If accepted for publication, your response will be hyperlinked to the article. To submit a comment, follow [this link](#). To read comments already accepted, follow [this link](#).

LITERATURE CITED

- Arroyo, M. T. K., R. Primack, and J. J. Armesto.** 1982. Community studies in pollination ecology in the high temperate Andes of central Chile. I. *American Journal of Botany* **69**:82-97.
- Arroyo, M. T. K., R. Primack, and J. J. Armesto.** 1985. Community studies in pollination ecology in the high temperate Andes of central Chile. II. *Plant Systematics and Ecology* **149**:187-204.
- Bañkowska, R.** 1980. Fly communities of the family Syrphidae in natural and anthropogenic habitats of Poland. *Memorabilia Zoologica* **33**:3-93.
- Bañkowska, R.** 1981. Hover flies (Diptera, Syrphidae) of Warsaw and Mazovia. *Memorabilia Zoologica* **35**:57-78.
- Batra, S. W. T.** 1995. Bees and pollination in our changing environment. *Apidologie* **26**:361-370.
- Boyle, R. M. D., and B. J. R. Philogène.** 1983. The native pollinators of an apple orchard: variations and significance. *Journal of Horticultural Science* **58**:355-363.
- Buchmann, S. L., and G. P. Nabhan.** 1996. *The forgotten pollinators*. Island Press, Washington, D.C., USA.
- Burgett, M.** 1980. Pollination of parsley (*Petroselinum crispum*) grown for seed. *Journal of Apicultural Research* **19**:79-82.

- Campbell, D. R., and A. F. Motten.** 1985. The mechanism of competition for pollination between two forest herbs. *Ecology* **66**:554-563.
- Day, M. C.** 1991. *Towards the conservation of aculeate Hymenoptera in Europe*. Council of Europe Press, Strasbourg, France.
- Disney, R. H. L.** 1986. Assessments using invertebrates: posing the problem. Pages 271-293 in M. B. Usher, editor. *Wildlife conservation evaluation*. Chapman and Hall, New York, New York, USA.
- Downes, J. A.** 1965. Adaptations of insects in the Arctic. *Annual Review of Entomology* **10**:257-274.
- Elberling, H., and J. M. Olesen.** 1999. The structure of a high latitude plant-flower visitor system: the dominance of flies. *Ecography* **22**:314-323.
- Ellis, W. N., and A. C. Ellis-Adam.** 1993. To make a meadow it takes a clover and a bee: the entomophilous flora of N.W. Europe and its insects. *Bijdragen tot de Dierkunde* **63**:193-200.
- Faegri, K., and L. van der Pijl.** 1979. *The principles of pollination ecology*. Pergamon Press, Oxford, UK.
- Flint, J. H., editor.** 1963. The insects of the Malham Tarn area. *Proceedings of the Leeds Philosophical and Literary Society, Science Section* **9**(2):15-91. [Cited in: R.H.L. Disney (1986).]
- Gauld, I. D., N. M. Collins, and M. G. Fitton.** 1990. *The biological significance and conservation of Hymenoptera in Europe*. Council of Europe, Strasbourg, France.
- Herrera, C. M.** 1988. Variation in mutualisms: the spatio-temporal mosaic of a pollinator assemblage. *Biological Journal of the Linnean Society* **35**:95-125.
- Hocking, B.** 1968. Insect-flower associations in the high Arctic with special reference to nectar. *Oikos* **19**:359-388.
- Inoue, T., M. Kato, T. Kakutani, T. Suka, and T. Itino.** 1990. Insect-flower relationship in the temperate deciduous forest of Kibune, Kyoto: An overview of the flowering phenology and the seasonal pattern of insect visits. *Contributions from the Biological Laboratory, Kyoto University* **27**:377-463.
- Inouye, D. W., and G. H. Pyke.** 1988. Pollination biology in the Snowy Mountains of Australia: comparisons with montane Colorado, USA. *Australian Journal of Ecology* **13**:191-210.
- Jarlan, A., D. DeOliveira, and J. Gingras.** 1997a. Pollination by *Eristalis tenax* (Diptera: Syrphidae) and seed set of greenhouse sweet pepper. *Horticultural Entomology* **90**:1646-1649.
- Jarlan, A., D. DeOliveira, and J. Gingras.** 1997b. Effects of *Eristalis tenax* (Diptera: Syrphidae) pollination on characteristics of greenhouse sweet pepper fruits. *Horticultural Entomology* **90**:1650-1654.
- Kakutani, T., T. Inoue, M. Kato, and H. Ichihashi.** 1990. Insect-flower relationship in the campus of Kyoto University, Kyoto: an overview of the flowering phenology and the seasonal pattern of insect visits. *Contributions from the Biological Laboratory, Kyoto University* **27**:465-521.
- Kato, M., T. Kakutani, T. Inoue, and T. Itino.** 1990. Insect-flower relationship in the primary beech forest of Ashu, Kyoto: an overview of the flowering phenology and the seasonal pattern of insect visits. *Contributions from the Biological Laboratory, Kyoto University* **27**:309-375.
- Kearns, C. A.** 1990. *The role of fly pollination in montane habitats*. Dissertation. University of Maryland, College Park, Maryland, USA.

- Kearns, C. A., and D. W. Inouye.** 1994. Fly pollination of *Linum lewisii* (Linaceae). *American Journal of Botany* **8**: 1091-1095.
- Kearns, C. A., D. W. Inouye, and N. M. Waser.** 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics* **29**: 83-112.
- Kevan, P. G.** 1972. Insect pollination of high Arctic flowers. *Journal of Ecology* **60**: 831-847.
- Kevan, P. G., and H. G. Baker.** 1983. Insects as flower visitors and pollinators. *Annual Review of Entomology* **28**: 407-445
- Larson, B. M. H., P. G. Kevan, and D. W. Inouye.** 2001. Flies and flowers: I. The taxonomic diversity of anthophilous pollinating flies. *Canadian Entomologist*, in press.
- Levesque, C. M., and J. F. Burger.** 1982. Insects (Diptera, Hymenoptera) associated with *Minuartia groenlandica* (Caryophyllaceae) on Mount Washington, New Hampshire, U.S.A., and their possible role as pollinators. *Arctic and Alpine Research* **14**: 117-124.
- Mani, M. S.** 1968. *Ecology and biogeography of high altitude insects*. Dr. W. Junk, The Hague, The Netherlands.
- Manning, J. C., and P. Goldblatt.** 1995. Cupid comes in many guises. *Veld and Flora* **81**: 50-53.
- Marlin, J. C., and W. E. LaBerge.** 2001. The native bee fauna of Carlinville, Illinois, revisited after 75 years: a case for persistence. *Conservation Ecology* **5**(1):9. [online] URL: <http://www.consecol.org/Journal/vol5/iss1/art9>
- Matheson, A., S. L. Buchmann, C. O'Toole, P. Westrich, and I. H. Williams, editors.** 1996. *The conservation of bees*. Academic Press, London, UK.
- McCall, C., and R. B. Primack.** 1992. The influence of flower characteristics, weather, time of day, and season on insect visitation rates in three plant communities. *American Journal of Botany* **79**: 434-442.
- McGuire, A. D., and W. S. Armbruster.** 1991. An experimental test for reproductive interactions between two sequentially blooming *Saxifraga* species (Saxifragaceae). *American Journal of Botany* **78**: 214-219.
- Mesler, M. R., J. D. Ackerman, and K. L. Lu.** 1980. The effectiveness of fungus gnats as pollinators. *American Journal of Botany* **67**: 564-567.
- Moldenke, A. R.** 1975. Niche specialization and species diversity along a California transect. *Oecologia* **21**: 219-242.
- Moldenke, A. R.** 1976. California pollination ecology and vegetation types. *Phytologia* **34**: 305-361.
- Moldenke, A. R., and J. L. Neff.** 1974a. Studies on pollination ecology and species diversity of natural California plant communities. *IBP [International Biological Programme] Technical Report 74-14*. Volume II.
- Moldenke, A. R., and J. L. Neff.** 1974b. Studies on pollination ecology and species diversity of natural California plant communities. *IBP [International Biological Programme] Technical Report 74-14*. Volume III.
- Motten, A. F.** 1986. Pollination ecology of the spring wildflower community of a temperate deciduous forest. *Ecological Monographs* **56**: 21-42.
- Nye, W. P., and J. L. Anderson.** 1974. Insect pollinators frequenting strawberry blossoms and the effect of honey bees on yield and fruit quality. *Journal of the American Society for Horticultural Science* **99**: 40-44.

- Osborne, J. L., I. H. Williams, and S. A. Corbet.** 1991. Bees, pollination and habitat change in the European community. *Bee World* **72**:99-116.
- Owen, J., and F. S. Gilbert.** 1989. On the abundance of hoverflies (Syrphidae). *Oikos* **55**:183-193.
- Pellmyr, O., and J. N. Thompson.** 1996. Sources of variation in pollinator contribution within a guild: the effects of plant and pollinator factors. *Oecologia* **107**:595-604.
- Petanidou, T., and W. N. Ellis.** 1993. Pollinating fauna of a phryganic ecosystem: composition and diversity. *Biodiversity Letters* **1**:9-22.
- Pojar, J.** 1974. Reproductive dynamics of four plant communities of southwestern British Columbia. *Canadian Journal of Botany* **52**:1819-1834.
- Primack, R. B.** 1978. Variability in New Zealand montane and alpine pollinator assemblages. *New Zealand Journal of Ecology* **1**:66-78.
- Primack, R. B.** 1983. Insect pollination in the New Zealand mountain flora. *New Zealand Journal of Botany* **21**:317-333.
- Reed, C.** 1995a. Species richness of insects on prairie flowers in Southeastern Minnesota. Pages 103-105 in *Proceedings of the 14th Annual North American Prairie Conference*. Kansas State University, Manhattan, Kansas, USA.
- Reed, C.** 1995b. Insects surveyed on flowers in native and reconstructed prairies (Minnesota). *Restoration and Management Notes* **13**:210-212.
- Richards, A. J.** 1986. *Plant breeding systems*. George Allen and Unwin, Boston, Massachusetts, USA.
- Robertson, C.** 1929. *Flowers and insects lists of visitors to four hundred and fifty-three flowers*. Science Press Printing, Lancaster, Pennsylvania, USA.
- Samways, M. J.** 1994. *Insect conservation biology*. Chapman and Hall, New York, New York, USA.
- Schemske, D. W., and C. C. Horvitz.** 1989. Temporal variation in selection on a floral character. *Evolution* **43**:461-465.
- Shaw, D. C., and R. J. Taylor.** 1986. Pollination ecology of an alpine fell-field community in the North Cascades. *Northwest Science* **60**:21-31.
- Siemann, E., D. Tilman, and J. Haarstad.** 1996. Insect species diversity, abundance and body size relationships. *Nature* **380**:704-706.
- Thomson, J., and B. Thomson.** 1992. Pollen presentation and viability schedules in animal-pollinated plants: consequences for reproductive success. Pages 1-24 in R. Wyatt, editor. *Ecology and evolution of plant reproduction: new approaches*. Chapman and Hall, New York, New York, USA.
- Toft, C. A.** 1983. Community patterns of nectivorous adult parasitoids (Diptera, Bombyliidae) on their resources. *Oecologia* **57**:200-215.
- Torchio, P. F.** 1990. Diversification of pollination strategies for U.S. crops. *Environmental Entomology* **19**:1649-1656.
- Waser, N. M., L. Chittka, M. V. Price, N. M. Williams, and J. Ollerton.** 1996. Generalization in pollination

systems, and why it matters. *Ecology* **77**:1043-1060.

Watanabe, M. E. 1994. Pollination worries rise as honey bees decline. *Science* **265**:1170.

Whittaker, R. H. 1952. A study of summer foliage insect communities in the Great Smoky Mountains. *Ecological Monographs* **22**:1-43.

Williams, P. H. 1986. Environmental change and the distributions of British bumble bees (*Bombus* Latr.). *Bee World* **67**:50-61.

Williams, B., R. Dransfield, and R. Brightwell. 1990. Monitoring tsetse fly populations. I. The intrinsic variability of trap catches of *Glossina pallidipes* at Nguruman, Kenya. *Medical and Veterinary Entomology* **4**:167-179.

Wolda, H. 1992. Trends in abundance of tropical forest insects. *Oecologia* **89**:47-52.

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