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Generalization in Pollination Systems, and Why it Matters

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Editor's Note

Many of the most elaborate examples of extreme adaptive specialization can be found in pollination systems. The interactions among flowering plants and insects, for example, are textbook illustrations of the coevolutionary process and prompted Darwin to write one of his most influential books, *The Various Contrivances by Which Orchids are Fertilized by Insects*. For over a century now evolutionary biologists have considered extreme specialization in pollination systems the common outcome of selection, with generalization only a rarity. Major morphological features of flowers have been selectively driven through specialization into suites of canalized characters forming "pollination syndromes" that are adapted to specific classes of pollen vector. Likewise, pollinators exhibit extreme specialization in the flowers they will attempt to exploit for critical floral resources. So goes the story.

But not so, according to Waser and colleagues. They feel extreme specialization may not be as ubiquitous a phenomenon as we believe, and that generalization in pollination systems may be as important an evolutionary outcome as specialization. In a very thorough review using broad comparisons across large floras, they find wide evidence for generalization within pollinator-plant interactions. They indicate the consequences of generalization for broader ecological interactions and raise a general caveat against assuming specialization as the inevitable outcome of selection among interacting species. Their article should reopen and stimulate further discussion on the old problem of adaptive specialization vs. generalization in ecological interaction.

Leslie A. Real

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GENERALIZATION IN POLLINATION SYSTEMS, AND WHY IT MATTERS¹

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Abstract

One view of pollination systems is that they tend toward specialization. This view is implicit in many discussions of angiosperm evolution and plant-pollinator coevolution and in the long-standing concept of "pollination syndromes." But actual pollination systems often are more generalized and dynamic than these traditions might suggest. To illustrate the range of specialization and generalization in pollinators' use of plants and vice versa, we draw on studies of two floras in the United States, and of members of several plant families and solitary bee genera. We also summarize a recent study of one local flora which suggests that, although the colors of flowers are aggregated in "phenotype space," there is no strong association with pollinator types as pollination syndromes would predict. That moderate to substantial generalization often occurs is not surprising on theoretical

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grounds. Plant generalization is predicted by a simple model as long as temporal and spatial variance in pollinator quality is appreciable, different pollinator species do not fluctuate in unison, and they are similar in their pollination effectiveness. Pollinator generalization is predicted when floral rewards are similar across plant species, travel is costly, constraints of behavior and morphology are minor, and/or pollinator lifespan is long relative to flowering of individual plant species. Recognizing that pollination systems often are generalized has important implications. In ecological predictions of plant reproductive success and population dynamics it is useful to widen the focus beyond flower visitors within the "correct" pollination syndrome, and to recognize temporal and spatial fluidity of interactions. Behavioral studies of pollinator foraging choices and information-processing abilities will benefit from understanding the selective advantages of generalization. In studies of floral adaptation, microevolution, and plant speciation one should recognize that selection and gene flow vary in time and space and that the contribution of pollinators to reproductive isolation of plant species may be overstated. In conservation biology, generalized pollination systems imply resilience to linked extinctions, but also the possibility for introduced generalists to displace natives with a net loss of diversity.

Key words: behavior; behavioral constraints of pollinators; evolution; foraging theory; generalization in pollination systems; interaction-web connectance; mutualism; plant-animal interaction; pollination syndromes; solitary bees; specialization; surveys of local floras.

Relations between flowers and insect pollinators are archetypes of the results of coevolutionary interactions . . . Constant pollination might allow a maximum number of plant species . . . since . . . each plant species might have an efficient pollinator in spite of relatively high species density.

Crepet 1983:29–30

The flowers of each species are adapted in shape, structure, color, and odor to the particular pollinating agents on which they depend . . . Evolving together, the plants and their pollinators become more finely tuned to each other's peculiarities . . .

Keeton and Gould 1993:476

Collectors' notes are worthless as data of anthecology because the collector is looking out for particular kinds of insects and not for all the kinds which occur on the flowers. Robertson 1928:4–5

Die Farbe bildet ein Merkzeichen, aber keine Anziehung an und für sich für das Insekt [Color constitutes a cue, but no attraction in and of itself for an insect]. Forel 1910:194

Introduction

A pervasive idea in pollination biology is that the interactions between plants and animal pollinators tend to be specialized. For example, specialization is implied by the concept of "pollination syndromes," which appears as an organizing principle for the field in textbooks and in the primary literature (van der Pijl 1961, Baker and Hurd 1968, Keeton and Gould 1993, Lunau 1993, Hodges and Arnold 1994). The pollination syndromes are suites of floral traits proposed to reflect adaptations to one or another pollinator type roughly at the level of orders (e.g., beetles vs. butterflies vs. bees) or above (e.g., beetles vs. birds). Indeed, because floral traits often distinguish angiosperm species, pollinator specialization has long been considered critical to plant speciation and evolutionary radiation (Grant 1949, Baker 1963, Grant and Grant 1965, Stebbins 1970, Crepet 1983). Along with this, some workers have proposed a general evolutionary trend toward specialization (Stebbins 1970, Crepet 1983, 1984), with increasingly tight coevolution of plants and pollinators (Gilbert and Raven 1975), whose evolutionary best interests might even converge (Howell 1979, Kevan and Baker 1983).

These ideas are tidy, and enjoy several sources of support. Dramatic specialization does occur in some pollination systems. Many biologists perceive repeated patterns in the phenotypic expression of flowers, as required by the pollination syndrome concept—suggesting that the longevity of this concept (which dates to Delpino 1868–1875) owes something to biological reality. And specialization and tight coevolution could explain the rapid radiation of angiosperms and taxa of animal pollinators during the cenozoic (Crepet 1983, Kiester et al. 1984, Eriksson and Bremer 1992).

At the same time, there are problems. Nature presents us with coevolution that often is diffuse (Janzen 1980, Schemske 1983, Howe 1984), and with many generalized pollination systems in both temperate and tropical habitats (Waser 1983, Feinsinger 1987, Roubik 1992, Renner and Feil 1993, Waser and Price 1993). Geographic ranges of given plants and pollinators rarely correspond closely, indicating that their interactions are not obligate; indeed, species of plants (including those incapable of selfing) and of pollinators that have invaded new geographic areas often are successful even when their ancestral mutualists were left behind (Cox 1983, Lord 1991, Forster 1994, Herrera 1995). On closer examination, even figs, yuccas, and their visitors may not involve absolutely obligate interactions (Wiebes 1979, Pellmyr and Thompson 1992, Patel et al. 1993, Dodd and Linhart 1994).

To us the issue of how richly connected plants and pollinators are seems fundamental, but all too little

discussed and explored. In this paper we pose two related questions. First, what does the empirical evidence actually suggest about specialization and generalization? To provide a preliminary answer, we draw on several classical surveys of pollination and of plant and insect taxa, and on a new study of our own. We conclude that pollination systems range from fairly specialized to very generalized, with moderate generalization the rule rather than the exception (we are forced to describe this continuum with the terms "specialization" and "generalization," and return to limitations of this dichotomy under *Conclusions and implications*). Second, what is the theoretical expectation? Here we draw on a simple model of plant fitness and on foraging theory, both of which suggest that conditions commonly will favor generalization in pollination systems. We also discuss evidence that this conclusion is not jeopardized by constraints of behavior, morphology, or physiology. We end by contemplating why it is important for biologists to recognize the generalized nature and flexibility of many pollination systems.

Generalization in Plant-Pollinator Interactions

Ideals to contemplate

To assess the degree of specialization or generalization we need to know several things. First, we would like to characterize pollination from the point of view of a plant species, recording visitors and assessing which ones pollinate and how effectively (e.g., Motten et al. 1981, Tepedino 1981a, Herrera 1987, Waser and Price 1990). We also would like to understand the pollinator's perspective, characterizing its flower choices in terms of energy and other criteria (e.g., Strickler 1979, Stucky 1984, Pleasants and Waser 1985, Duffield et al. 1993). Starting with one or a few species, however, should soon lead us to a web of interactions, unless plants and pollinators are obligately related. We would like to characterize this web, and to know how it changes as we sample larger temporal and spatial domains, and thus ecological contexts (see also Thompson 1994).

Fragmentary studies

Most pollination studies to date, our own included, provide only a fraction of the total perspective just outlined. Despite their limitations, such studies often convey the impression of generalization and fluidity. Plants often employ a variety of pollinating agents (e.g., Robertson 1928, Schremmer 1953, Beattie 1971, Primack 1979, Waser 1982, Kephart 1983, Bullock et al. 1989, Carpenter 1989, Pettersson 1991, Roubik 1992, Erhardt 1993), and mixtures of abiotic and biotic agents (e.g., wind and insects) are not taboo (Knuth

1908, Robertson 1928, Adams et al. 1981, Anderson et al. 1988, Cane and Payne 1993, Renner and Feil 1993). Generalization is even greater when one looks at the visitors to a given plant species over time and space, whether on a local or geographic scale (Herrera 1988, 1996, Horvitz and Schemske 1990, Warnke et al. 1993, Kwak 1994, Thompson 1994, Bronstein 1995, Fishbein and Venable 1996). In part this reflects temporal fluctuation in the local abundance, or even presence/absence, of given pollinator species; such fluctuation can be dramatic (Petanidou and Ellis 1993, Stubblefield et al. 1993). Pollinators in temperates and tropics likewise tend to visit multiple plant species in a single genus, or of diverse genera and families (e.g., Feinsinger 1983, 1987, Schemske 1983, Sommeijer et al. 1983, Waser 1983, Absy et al. 1984, Ackerman 1985, Pedro 1993, Scott et al. 1993).

Surveying an entire pollination assemblage

The studies just cited usually focus on one or a few plant or animal species at a single time and place, and so might represent a biased sample of all pollination systems. To reduce the chance of bias we advocate surveys of entire local assemblages of plants and pollinators (a daunting task!), without any prior selection of species. Several of the studies cited above and others analyzed by Jordano (1987) in fact explore portions of such assemblages. However, the treatment in all cases is circumscribed by some limit of taxonomic focus (for example on "hummingbird-pollinated" flowers, whose insect visitors are ignored). We know of only a few studies that treat all or most of a local flora and/or its pollinating fauna.

Robertson (1928) surveyed the entire angiosperm flora around Carlinville, Illinois, USA, and distinguished flower visitors that pollinated from those that did not. The 375 native species received visits from as few as one pollinator species each, and as many as 298 species in 84 genera, with a mean (median) of 33.5 (18) pollinator species per plant species (Fig. 1). Furthermore, 91% of all plant species were visited by more than a single animal species and thus were at least somewhat generalized.

Several surveys are available for faunas of solitary bees, which are major pollinators in many ecosystems. These surveys suggest that specialization, expressed as "oligolecty," is rare in tropical forests, more common in temperate regions, and predominant in deserts (Table 1). However, there are major caveats. First, oligolecty is defined as specialization at the level of plant genus or family, not species. It also refers only to plants visited for pollen, whereas solitary bees also visit plants for nectar and pollinate them in the process. Even the most extreme oligolectes appear to be

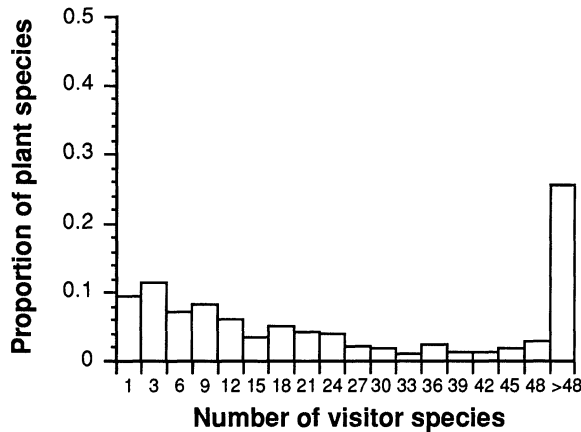


FIG. 1. Pollinator affinities in the Carlinville, Illinois (USA) flora, from records in Robertson (1928). Frequency distribution of the proportions of 375 native plant species receiving pollination visits from different numbers of animal species.

generalized to nectar sources (Westrich 1989). Finally, those few bee species that appear to visit only a single species for pollen in a given area sometimes visit other species in other parts of their geographic range (Cross and Bohart 1960, Eickwort and Eickwort 1969, Minckley et al. 1994), and stray from their speciality when it is in short supply (Michener and Rettenmeyer 1956, Thorp 1969, Cruden 1972, Michener 1979, Adams et al. 1981, Cane and Payne 1988). Thus, the surveys of solitary bees actually suggest again that some degree of generalization and opportunism is common.

A final survey, unique as far as we know in providing tabulations both by plants and animals, comprised 94 native plant species in montane conifer forest and grassland on Pikes Peak, Colorado, USA. These

TABLE 1. Relative abundances of oligolectic bees, taken to be specialists (but see *Generalization in plant-pollinator interactions: Surveying an entire pollination assemblage* for caveats), in some different biomes and areas of the Americas. Data are from Heithaus (1979), Michener (1979), Moldenke (1979), Absy et al. (1984), and de Mezes Pedro (1993).

Biome or Area	Total no. bee species	No. oligo-lectic	% oligo-lectic
Desert	890	592	66.5
Great Basin	333	165	49.5
Great Plains	500	184	36.8
Pacific Northwest	425	104	24.5
Southern forest	280	63	22.5
Rocky Mountain	500	90	18.0
Tundra/Muskeg	84	13	15.5
Tropical wet forest	22	1	5.0
Tropical grassland	192	3	1.5

species were observed by Clements and Long (1923) to receive visits from as few as 1 animal species, and as many as 62 species in 30 genera. The frequency distribution of visitors was right-skewed (Fig. 2A), with means (medians) of 9.8 (4) visitor species and 6.1 (3) genera per plant species; 80% of all plant species were visited by >1 animal species. By comparison, the 268 native animal pollinators were observed to visit as few as 1 and as many as 37 plant species in 32 genera (Fig. 2B), with means (medians) of 3.3 (1) plant species and 2.8 (1) plant genera visited; 48% of all animal species visited >1 plant species. The overall connectance of the interaction web (the fraction of all possible plant-pollinator interactions actually realized) was 3.6%. This is lower than the average connectance of 29.4% reported by Jordano

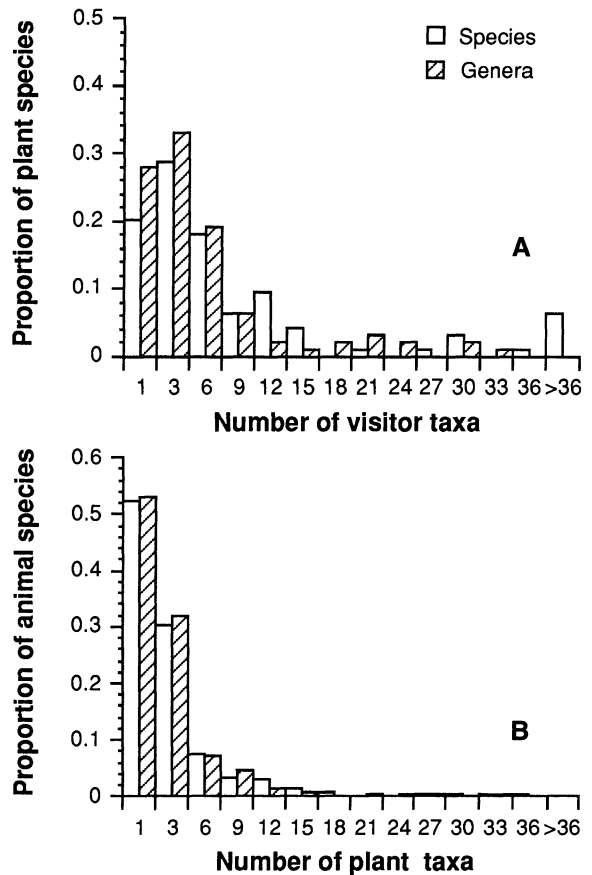


FIG. 2. Plant and pollinator records from Pikes Peak, Colorado (USA), from records in Clements and Long (1923). (A) Frequency distribution of the proportions of 94 native plant species receiving visits from different numbers of animal species and genera. (B) Frequency distribution of the proportions of 268 native animal species visiting different numbers of plant species and genera.

(1987), but the small fragments of pollination webs that he considered averaged only 44 species of animals and plants combined (hereafter “*S*”), compared to 359 at Pikes Peak. For connectance to stay constant as *S* increases requires that interactions per species rise approximately as S^2 . Whereas entire food webs may behave this way within limits (Martinez 1992), connectance does appear to decline with *S* in pollination webs (Jordano 1987). At 3.6% the Pikes Peak system actually is substantially more strongly connected than the value of 0.1% predicted from an empirical relationship derived by Jordano (1987). This suggests that fragments of pollination webs if anything underestimate the connectance and generalization in entire assemblages—just as expected from the limited taxonomic focus inherent in such fragments.

Surveys by plant or animal taxon

Another way to reduce bias in examining pollination interactions is to characterize them at the level of higher plant or animal taxon, without any prior selection of species. Some published pollination studies already focus at the level of plant or animal family or other taxon.

To illustrate, we begin with examples of three angiosperm families. We have extracted information on European members of the buttercup family (Ranunculaceae) and orchid family (Orchidaceae) from Knuth (1908 and 1909, respectively), and on North American members of the phlox family (Polemoniaceae) from Grant and Grant (1965). These choices represent respectively a large “primitive” family, a large “advanced” family, and a small “advanced” family (sensu Stebbins 1974); the latter two usually are presumed to be specialized in pollination. For each family we surveyed the published source in question one species at a time, tabulating all recorded flower visitors. We excluded any case where a plant species was examined outside its natural habitat. The results resemble those from the Carlinville and Pikes Peak floras. The 39 members of the Ranunculaceae received visits from as few as 1 animal species, and as many as 53 species in 29 genera (Fig. 3A), with means (medians) of 11.8 (10) visitor species and 8.8 (6) genera per plant species; 95% of all plant species received visits by >1 animal species. The 11 members of the Orchidaceae received visits from as few as 2 species in two genera and as many as 15 species in 13 genera, with means (medians) of 7.9 (8) visitor species and 5.0 (2) genera per plant species; none was limited to a single animal species (Fig. 3B). The 73 members of the Polemoniaceae received visits from as few as 1 species and as many as 39 species in 17 genera, with means (medians) of 6.5 (4) visitor species and 5.4 (3) genera per plant

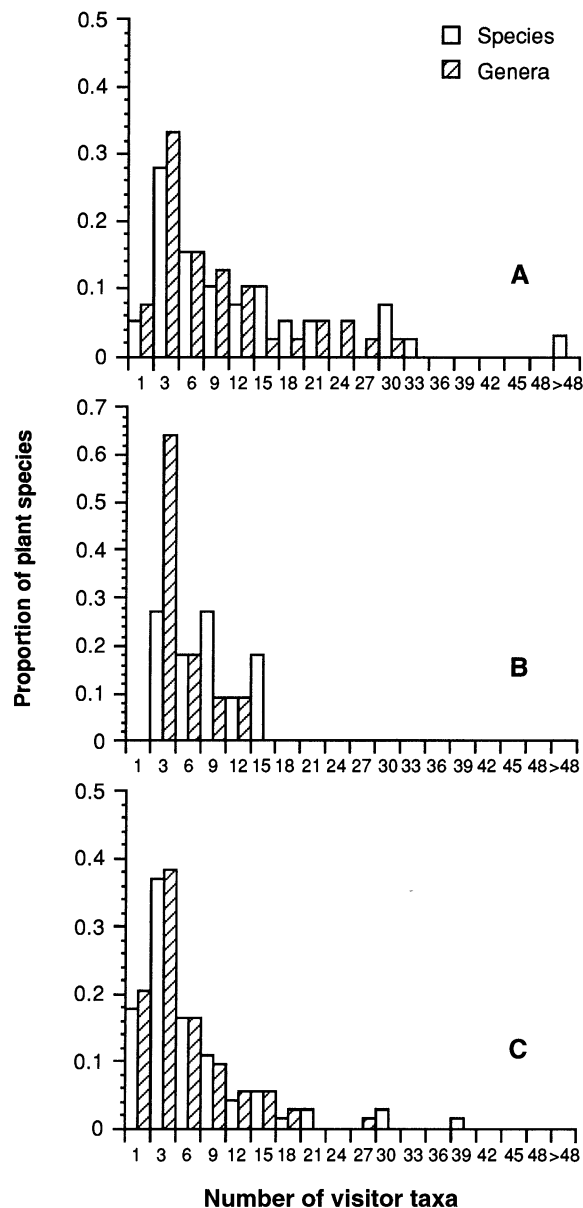


FIG. 3. Pollinator affinities of members of different plant families, shown as frequency distributions of the proportions of plant species receiving visits from different numbers of animal species and genera. (A) Thirty-nine European members of the Ranunculaceae, from records in Knuth (1908). (B) Eleven European members of the Orchidaceae, from records in Knuth (1909). (C) Seventy-three North American members of the Polemoniaceae, from records in Grant and Grant (1965).

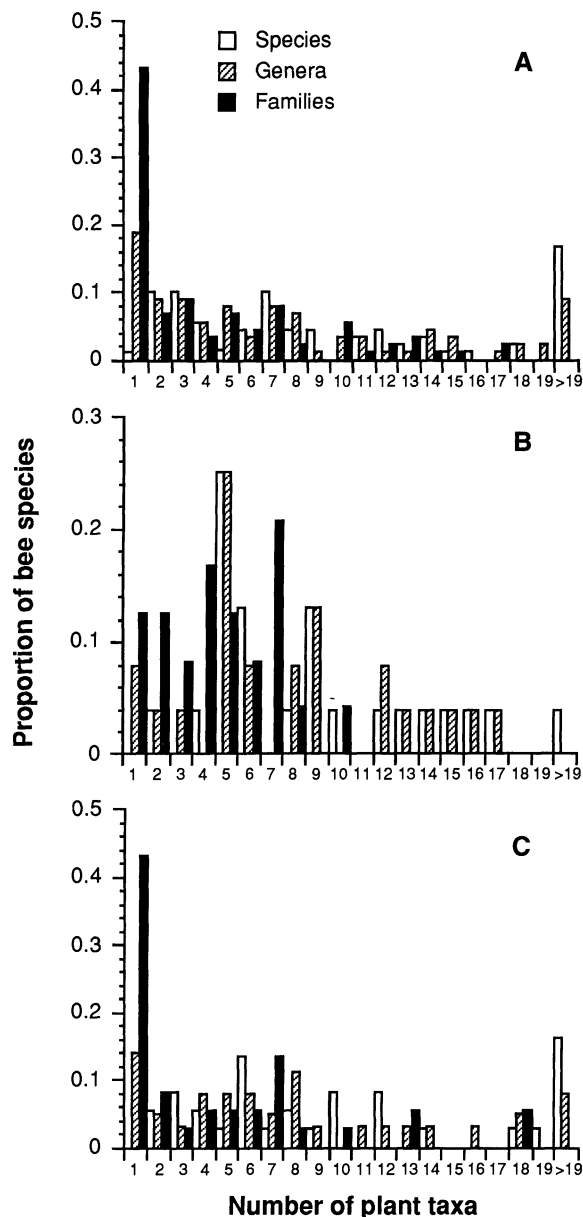


FIG. 4. Flower affinities of members of three different genera of solitary bees, shown as frequency distributions of the proportions of bee species visiting different numbers of plant species, genera, and families, from records in Westrich (1989). (A) Ninety members of the genus *Andrena*. (B) Twenty-four members of the genus *Hylaeus*. (C) Thirty-seven members of the genus *Osmia*.

species; 82% received visits from >1 animal species (Fig. 3C).

Turning to pollinators, we again chose bees as our focus. Heithaus (1979) used published records to estimate that members of the most specialized bee fam-

ily, the Colletidae, visited on average 3.4 plant families for pollen or nectar; members of the most speciose family, the Halictidae, visited on average 8.4 plant families, and members of the most generalized family, the Apidae, visited on average 18.4 plant families. These numbers suggest substantial generalization, but at a crude taxonomic resolution. A finer resolution is provided by Westrich's (1989) monograph on bees of southwestern Germany. From the 26 genera containing more than 5 species each we randomly selected *Andrena*, *Hylaeus*, and *Osmia*, representing three different families (respectively Andrenidae, Colletidae, and Megachilidae). We tabulated the numbers of plant families, genera and species visited by each bee species. One species of *Andrena* and two of *Osmia* were apparently monolectic (obligate to a single plant species as pollen source) over the geographic range studied by Westrich. Otherwise, generalists predominated. The 90 species of *Andrena* visited means (medians) of 9.4 (6) plant species, 7.7 (5) genera, and 4.1 (2) families (Fig. 4A). The corresponding values were 8.8 (7) species, 8.0 (7) genera, and 4.6 (4.5) families for the 24 species of *Hylaeus* (Fig. 4B); and 10.9 (8) species, 8.5 (6) genera, and 3.9 (2) families for the 37 species of *Osmia* (Fig. 4C). Interestingly, a recent phylogenetic mapping of pollen use within the tribe Anthidiini of the Megachilidae suggests that polylecty (generalization in plants visited for pollen) has evolved repeatedly from oligolecty, but not vice versa (Müller 1996).

Biases in surveys

We recognize that conclusions based on surveys are imperfect. The problem that comes immediately to mind is that surveys are likely to overestimate the degree of generalization. Flower visitation is not a synonym for pollination, and even if non-pollinating visitors are excluded (as in Robertson 1928), the remaining visitors will differ in pollination efficiency (see citations in *Introduction*). Similarly, a given insect or other animal recorded at a given flower may visit only incidentally. Ignoring these details will exaggerate the connectance of plant-pollinator interactions. However, there also are counterbalancing biases towards *underestimating* generalization and opportunism in pollination mutualisms. One of these is that surveys almost invariably are very restricted in temporal and spatial dimensions. But pollination interactions vary along these dimensions, as already noted, so surveys will underestimate their complexity. Specialization of a particular pollinator group, the solitary bees, is overestimated by the practice of studying pollen collection, and the paucity of records of plants visited for nectar. Finally, there may be a widespread

unconscious bias to ignore visitors that seem “improper” under the paradigm of pollination syndromes (see the quotation from Robertson [1928] at the beginning of this paper). As a first approximation, the presence of biases in both directions suggests that survey results may reflect large-scale patterns with reasonable accuracy.

Consider two examples that illustrate bias toward underestimating the degree of generalization. Two of us (N. M. Waser and M. V. Price) have studied pollination of the montane plant *Ipomopsis aggregata* for 20 yr. Grant and Grant (1965) list eight species of flower visitors in seven genera, to which Waser (1978, 1982) adds at least four species in four genera known to transfer pollen (*Hyles lineata*, *Bombus appositus*, *Papilio rutulus*, *Halictus* sp.). Clements and Long (1923) list only two species in the genus *Halictus*—thereby omitting entirely the hummingbird pollinators of this classical “hummingbird syndrome” species. And, even a combined listing of ≈ 12 pollinator species must be incomplete given the limited sample of sites and years. Thus it appears that Grant and Grant (1965) underestimated the number of species-level pollination mutualisms in which *I. aggregata* engages by at least 33%, and Clements and Long (1923) underestimated by at least 83%. As an animal example, consider the Broad-tailed Hummingbird, *Selasphorus platycercus*, reported by Clements and Long (1923) to pollinate 7 plant species and by Waser (1983) to regularly visit an additional 12 species in eight families (most of which do not conform to a “hummingbird pollination syndrome”). Clements’ and Long’s list comprises only 37% of the total of 19 species, and this total does not come close to encompassing the floral diet of broad-tails across years and sites.

A different approach: surveys of floral phenotype space

The concept of pollination syndromes contributes to an impression of specialization in pollination systems. Do patterns in nature actually conform to those predicted by syndromes; i.e., do flowers form clusters in “phenotype space” that correspond to visitation by major pollinator groups? Few studies seem to have addressed this issue. Baumberger (1987) analyzed the corolla lengths of over 1000 “bird syndrome” flowers worldwide, and found that values cluster around an intermediate length (16–26 mm) that matches bill length in three major families of nectar-feeding birds (mean ≈ 19 mm). Unfortunately, the definition of bird flowers along syndrome lines contributes a circularity.

To avoid this it is important to sample plant species at random or to sample an entire flora. One of us (L. Chittka) adopted the latter approach in a study of flow-

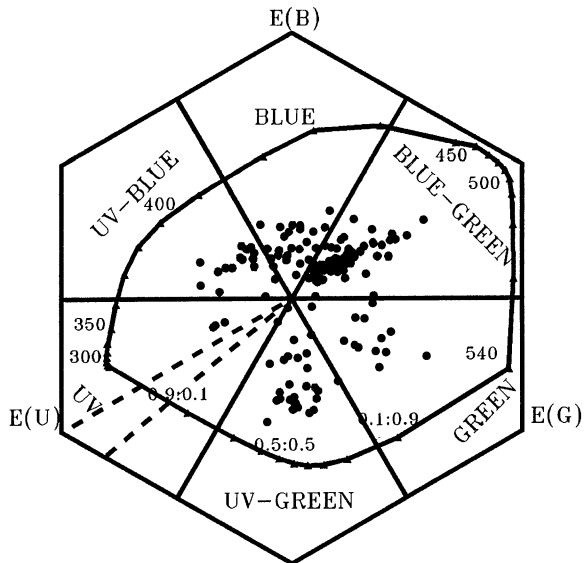


FIG. 5. The positions of 154 flowers from the nature reserve near Berlin, plotted in a hexagonal color space. Points in the upper part of this space are bee blue colors, points in the lower left corner are bee ultraviolet (UV) colors, etc. The irregular polygon within the hexagon connects the loci of monochromatic lights in 10-nm steps from 300 nm to 540 nm; its curved bottom segment connects the loci of 300 nm and 540 nm in nine mixtures of the two colors with ratios of 0.9:0.1, 0.8:0.2, . . . 0.1:0.9 (see Chittka 1992). One of the 10° sectors in which color loci were counted for Fig. 6 is indicated by dashed lines in the lower left (this particular sector contains no flowers).

er color, a central element of putative pollination syndromes. Five sites were chosen in a nature reserve near Berlin (Naturschutzgebiet Lange Dammwiesen), and flower colors of all 154 plant species were quantified by measuring their spectral reflectance from 300 to 700 nm. A point was then calculated for each flower in a hexagonal space that describes color as the visual system of honey bees and other bees will perceive it (Fig. 5). Angular position of a point in this color hexagon corresponds to hue (Wyszecki and Stiles 1982). To see whether flowers form clusters of similar hues we divided the space into sectors of 10° each and counted the number of plant species occupying each sector (see Chittka et al. 1994). Indeed, flowers did form distinct clusters at angular intervals of $\approx 60^\circ$ (Fig. 6). Furthermore, these clusters also are recognizable to other color vision systems (Chittka et al. 1994), including our own (Kevan 1978). However, the syndrome concept also would predict that different pollinators largely restrict their attention to different subsets of all clusters. To see if this was so, all visitors to flowers over a 1-yr period were identified at the level of insect order. Fig. 7 shows the percentages of

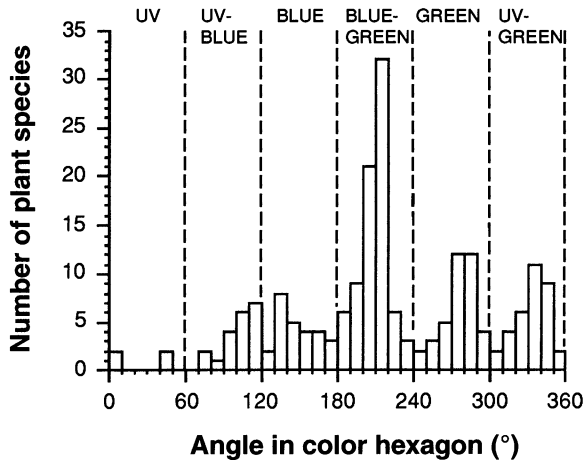


FIG. 6. The distribution of all flowers depicted in Fig. 5 in the 36 10° sectors of the color hexagon. Zero degrees represents the line separating the UV-green and UV portions of the hexagon (see Fig. 5).

different color categories visited by flies, beetles, butterflies, large bees (honey bees or larger), and small bees (smaller than honey bees). There were no statistical differences among these animal groups in the colors of flowers visited ($\chi^2 = 29.8$, $df = 20$, $P > 0.05$), or between the colors visited by any group and those available in the flora (in all cases $\chi^2 \leq 7.1$, $df = 5$, $P > 0.1$). To be sure, there were hints of classical syndromes: flies and beetles visited slightly more bee blue-green flowers (mostly human white), whereas large bees and butterflies visited more bee UV-blue and bee blue flowers (human blue, purple, pink, and violet). But these are only *trends*. For this flora, then, we reject the idea that clusters of flower colors represent syndromes by which plants address specific groups of potential visitors. Clustering in color space instead may mostly reflect constraints imposed by the chemistry of plant pigments (Chittka et al. 1994).

When Should Plants Generalize?

A short-term perspective

The empirical evidence suggests that pollination mutualisms often are diversified and opportunistic, and therefore constitute true food webs as opposed to food chains. Can we understand why this is so? We start by sketching out a basic model that considers the optimal diversity of pollinating animals from a plant's perspective. Our approach is similar to that in several previous models of ecological processes (e.g., Real 1980, Lacey et al. 1983, Real and Ellner 1992).

The model compares a phenotype that generalizes on two pollinator species with a phenotype that spe-

cializes. In any one flowering episode the fecundity of a generalist (hereafter its "fitness") is

$$W_G = N_1V_1g_1 + N_2V_2g_2, \quad (1)$$

where N_1 is the abundance of pollinator species 1, V_1 is the flower visitation rate per individual pollinator, and g_1 is the effectiveness of each visit, i.e., the degree to which it contributes to individual reproductive success. Terms subscripted with "2" refer to identical attributes of pollinator species 2. Now, imagine a rare mutation (for example in flower morphology and placement of stamens and/or pistils) that increases the effectiveness of species 1 by δ , and equally decreases that of species 2. This mutation involves the most complete possible trade-off in fitness value of the two pollinators to the plant, and represents the greatest possible increase in plant specialization. Its fitness is

$$W_{s,1} = N_1V_1(g_1 + \delta) + N_2V_2(g_2 - \delta). \quad (2)$$

Comparison of Eqs. 1 and 2 shows that the mutation for increased morphological specialization spreads if $W_{s,1} > W_G$, i.e., if $N_1V_1 > N_2V_2$. Thus, assuming that pollinators differ in abundance, a mutation that increases the efficiency of the most abundant visitor (with the larger product of N and V) will increase in frequency, even if in the process the plant becomes more specialized on that visitor. Similarly one can imagine a mutation (perhaps in reward or floral display) that enhances the attractiveness to one pollinator species, and thus its per-capita visitation rate, at the expense of reduced visitation by the other pollinator. The fitness of this mutation is

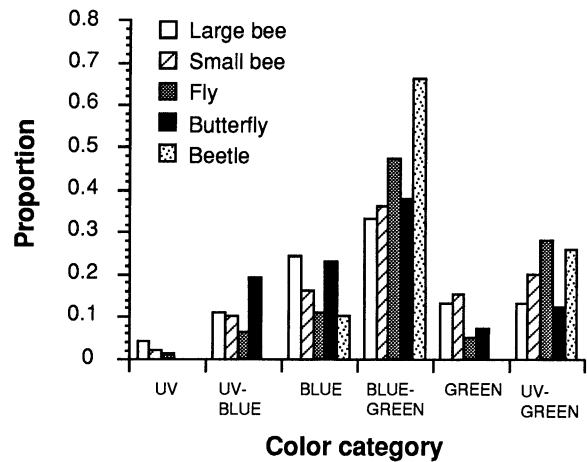


FIG. 7. The colors of flowers visited by different groups of insects. Histograms indicate the percentages of all plant species visited by a given insect group that fell into a given color category. For example, the highest stippled histogram shows that 66% of all plant species visited by beetles were in the bee blue-green category.

$$W_{s,1} = N_1(V_1 + \delta)g_1 + N_2(V_2 - \delta)g_2. \quad (3)$$

Comparison of Eqs. 1 and 3 shows that the mutation will spread if $N_1g_1 > N_2g_2$. Thus, assuming that pollinators differ in efficiency, a mutation that increases the attraction of the most efficient pollinator will spread, even at a loss of attraction to another visitor and thus a net increase in specialization.

A long-term perspective

So far, results of the model agree with the classical view that specialization on a single best pollinator is favored. What happens, however, when the abundances, per-capita visitation rates, or (perhaps less likely) the efficiencies of different pollinators (the N , V , and g terms) vary temporally, so that in the extreme the "best" pollinator changes across plant generations (e.g., Petanidou and Ellis 1993, Stubblefield et al. 1993)? The long-term fitness of plants is the geometric mean over generations (here we imply non-overlapping generations, but a similar argument applies for overlapping generations). An approximate equivalence is

$$W = \mu - [\text{var}(W)/(2\mu)], \quad (4)$$

where μ is the arithmetic mean fitness over n generations (i.e., $\mu = 1/n \sum W_i$, where i indexes generation), and $\text{var}(W)$ is the temporal variance in fitness (Lacey et al. 1983). Thus the arithmetic mean fitness is *discounted* by a function of the temporal variance.

Assume that a specialist plant genotype specializes completely on pollinator species 1, achieving short-term fitness of $W_{s,1} = k N_{1,i} V_{1,i} g_{1,i}$. The term " i " again refers to a specific generation, whereas k is a constant multiplier that describes the total gain in N , V , and/or g as a consequence of specializing on one pollinator. The fitness of the specialist over the long term, during which there is fluctuation in the product of N , V , and g (here symbolized as X), is

$$W_{s,1} = k E(X_1) - \{[k \text{var}(X_1)] / [2E(X_1)]\}, \quad (5)$$

where $E(X_1)$ is the expectation of X_1 , i.e., the arithmetic mean, as experienced by a generalist. The long-term fitness of the generalist is

$$W_G = E(X_1 + X_2) - \{[\text{var}(X_1) + \text{var}(X_2) + 2 \text{cov}(X_1, X_2)] / [2E(X_1 + X_2)]\}. \quad (6)$$

Under what conditions does the generalist outperform the specialist (i.e., $W_G > W_{s,1}$)? Eqs. 5 and 6 show that the answer depends on six parameters: arithmetic mean fitness contributions of each pollinator, variances in fitness contributions, the covariance in fitness contributions, and k , which encapsulates the

short-term benefit of specializing. There is no unique solution, but the inequality is favored if $\text{Cov}(X_1, X_2)$ is near zero, for example because the two pollinator populations fluctuate largely independently of one another; or is negative, for example because the populations fluctuate so as to compensate for one another.

The results of Pettersson (1991) are interesting in this context. He measured abundances of 26 moth species visiting *Silene vulgaris* over 4 yr. The eight most abundant species provided 75% of all pollination. The coefficient of variation (CV) in abundance of these species taken one at a time averaged 1.2, whereas the CV for the total of eight species was 0.4. This analysis is made without specific reference to the generation time of *S. vulgaris*, but it suggests that a generalist on many moth species (as *S. vulgaris* is) enjoys a lower variance discount than the average specialist would.

Conclusions

The model suggests that a plant may gain an advantage at any given time and place by specializing on the most abundant and/or efficient pollinator. But with temporal variation in pollinator services, specialization becomes less likely. This is true especially for plant species with few reproductive episodes and lacking other persistent life stages, since they face local extinction if they specialize on a pollinator that disappears for one or more years. Spatial variation in pollinator faunas, and in the identity of the "best" pollinator, also fosters greater generalization, at least at the plant species level.

We might therefore expect specialization on one or a few pollinators mostly in species that are large, long-lived, have many reproductive episodes, and/or have pollinators whose populations, for whatever mysterious reason, fluctuate little, so that the identity of the "best" pollinator tends to remain constant across years (this is not to imply that all such species will specialize). It is difficult to "test" these predictions because we lack a wealth of examples of obligate specialization across phylogenetically diverse plant taxa, but note that figs and yuccas do seem to fit the expectations.

When Should Pollinators Generalize?

A short-term perspective

There is a temporal element to the benefits required by both partners in a pollination mutualism. As we have just discussed, a plant gains reproductive success, measured over a long term. A pollinator usually gains food, which is critical to its survival and reproduction over both short and long terms.

A pollinator that forages efficiently is most likely to accumulate a surplus of energy and/or free time,

and thus to survive day-to-day, reach maturity, and reproduce successfully (Schoener 1971, Pyke 1984). What are the trade-offs to specialists vs. generalists? A foraging pollinator usually encounters a mixture of flower types (e.g., species). If energy rewards differ greatly among these types, costs of extracting them are high, and/or travel costs are low, a nearby flower with inferior rewards can profitably be skipped in favor of a superior distant flower, and a specialist that does so achieves the highest rate of reward intake. When rewards are similar and/or travel is costly, however, the optimal strategy for a pollinator with knowledge of upcoming options (an experienced pollinator or one that is "periscopic," i.e., can see flowers in advance of reaching them) is to generalize by including multiple flower types in its foraging path or itinerary (Stephens and Krebs 1986, Mitchell 1989). In fact, travel is energetically costly (Lasiewski 1963, Hainsworth and Wolf 1972, Heinrich 1979, Balderama et al. 1992), and floral rewards (at least nectar rewards) often are similar across species because pollinator foraging tends to equalize the effective value of all flowers (Heinrich 1976, Martínez del Rio and Eguarte 1987, Dreisig 1995):

A long-term perspective

Most flower-visiting animals face changing and variable resources. Even if the best short-term strategy is to visit only a single flower type, over the longer term a pollinator often should visit many types, for two reasons.

The first reason is seen by contemplating a necessary condition for visiting only a single flower type: that the pollinator's life cycle (at least the portion that depends on floral resources) be contained within the flowering period of the host plant. This condition may be met through a short pollinator life cycle and/or a long flowering period (perhaps comprised of staggered flowering episodes of individuals, as in figs; Bronstein et al. 1990, Patel et al. 1993), along with synchrony between the two (e.g., Galil 1977, Aker 1982, Dodd and Linhart 1994). More commonly, though, the condition is not met because pollinators, although short-lived, do not always achieve synchrony with their putative host (e.g., Cruden 1972); because pollinators (as individuals or colonies) outlive the flowering period of any one plant species (Free 1970, Heinrich 1979, Calder et al. 1983, Paton 1985, Boggs 1987); or because pollinators experience successive generations within a single growing season that encompasses the flowering of many plant species (e.g., Rozen 1958, Gregory 1963, Fleming 1970, Kislew et al. 1972, Estes and Thorp 1975).

The second reason to generalize over the long term

is more strictly analogous to the plant's perspective (see *When should plants generalize?*, above). The abundances of different flower species at a given site fluctuate across time periods (e.g., years; Waser and Real 1979, Tepedino and Stanton 1980), and abundances also vary through space. Thus even if pollinators specialize within a single season, variation in plant abundance may foster generalization of lineages or colonies, if not of individuals.

Behavioral, physiological, and morphological constraints

The exploitation of a flower requires behavioral abilities to detect signals and associate them with rewards, along with morphological and physiological abilities to extract and use the rewards. Are there constraints on these abilities that commonly force pollinators to specialize?

For the pollinator to add a novel flower to its diet it first must detect a novel floral signal. The most important signal modality in pollination systems is vision, and just as flowers are brightly colored, many pollinators are known to possess color vision. The trichromatic set of ultraviolet (UV), blue, and green receptors found in many bees and wasps appears to be an optimal system for flower color coding (Chittka and Menzel 1992), allowing its bearer in theory to discriminate on the order of 100 distinct flower colors (Chittka et al. 1993). Equivalent color receptors are found in some oligolectic solitary bees (Peitsch et al. 1992), suggesting that constraints on color vision cannot explain the putative specialization of these animals. The visual range of most other pollinating insects (e.g., flies, wasps, some butterflies and beetles) is similarly broad, often extending from near UV (around 320 nm) to near red (600–650 nm) (von Helversen 1972, Bernard and Stavenga 1979, Menzel and Backhaus 1991, Peitsch et al. 1992), and red flowers certainly are not "invisible to insects" as a pervasive truism of pollination biology claims (see also Pleasants and Waser 1985). Pollinating birds often surpass insects in possessing a broad spectral range (Goldsmith and Goldsmith 1979, Bennett and Cuthill 1994). Once it has detected a flower, the pollinator next must assess the quality of floral reward. Pollinators of several species are known to possess this ability (Forel 1910, Hainsworth and Wolf 1976, Heinrich et al. 1977, Menzel 1985, Haslett 1989, Harder 1990, Greggers and Menzel 1993) as well as the ability to match floral choices to rewards (Heinrich 1976, Pleasants 1981, Greggers and Menzel 1993, Dreisig 1995). Furthermore, pollinators such as hummingbirds, bees, flies, and butterflies can associate color signals with rewards (Goldsmith and Goldsmith 1979, Mazokhin-Porshnya-

kov et al. 1984, Waser and Price 1985, Chittka et al. 1988, 1992, Dukas and Real 1991, 1993, Menzel and Backhaus 1991, Weiss 1991, Troje 1993, Dukas and Waser 1994, Fukushi 1994); can do so quickly (e.g., Menzel 1967, 1985); and can remember the results (Lindauer 1963, Menzel 1967, 1985, Dukas and Real 1991). Although some insect pollinators do appear to have inborn preferences for certain floral signals (e.g., Chittka and Lunau 1992, Giurfa et al. 1995), close inspection suggests that these are rarely fixed and usually can be overwhelmed by the insects' capacities for learning and memory (Menzel 1985, Dobson 1987).

Differences in the morphology of pollinators, especially of the feeding apparatus (Beattie 1971, Wolf and Hainsworth 1972, Inouye 1980, Gilbert 1981, Dukas and Shmida 1989, Paton and Collins 1989, Feinsinger 1990, Grant and Temeles 1992), but also of other body parts (Feinsinger and Colwell 1978, Thorpe 1979, Collins and Paton 1989) and in overall body size, interact with the morphology and size of flowers to influence the efficiency of flower feeding. Conversely, these interactions influence the efficiency of pollination from the plant's viewpoint (Waser 1979, Nilsson et al. 1987, Armbruster 1990, Campbell et al. 1991). However, the classical view that constraints of morphological fit are strong enough to ensure specialization (Trelease 1881, Grant 1949, 1994)—strong enough for example to cause “mechanical” isolation of sympatric congeners—seems only rarely correct (e.g., Ramírez 1970).

Other potential constraints involve digestive physiology. For example, hummingbirds digest different sugars with somewhat different efficiencies (Martínez del Río 1990). Larval survival, growth rate, and size at pupation depend markedly on species of pollen for some solitary bees (Levin and Haydak 1957, Bohart and Youssef 1976). Those pollens that are of low nutritional value or even are toxic to one bee species, however, may support normal development of others (Tepedino 1981*b*). Such effects of diet on pollinator efficiency or fitness may somewhat limit the range of plant species used.

In summary, behavioral, morphological, and physiological constraints do exist, and will influence plant-pollinator associations on short and long time scales. However, these constraints rarely seem strong enough to restrict pollinators to a single plant species or only a few species.

Conclusions and Implications

Some philosophical points

Generalization—the use of several plant species by a pollinator and of several pollinator species by a plant—appears to be the rule rather than the exception.

Some readers will argue that this is not a new realization, and, indeed, many of the classic works that we cite as promoting specialization do contain caveats. But these caveats seem to have been largely ignored. Perhaps this reflects a very human desire to perceive nature as well ordered. Perhaps it derives in part from the unfortunate implication that specialization and generalization form a dichotomy. It would help if we could replace this implied dichotomy with a continuum, although the tendency to dichotomize and then to adopt one option runs deep in western culture (Hilborn and Stearns 1982). And, we have devised no attractive terminology to describe the continuum of pollination interactions (although at a community level the interaction-web connectance provides a descriptive metric, as long as one can correct for web size). Other readers may feel that we have wrongly rejected elements of the established paradigm: that there *are* detectable associations between plant phenotypes and pollinators (i.e., pollination syndromes); that more complex flowers within a plant family and more evolutionarily “advanced” plant families *are* more specialized, and so on. Our response is that much of the acceptance of these patterns has rested on a weak empirical foundation. Although, for example, our survey of small parts of three plant families suggests that members of the “primitive” Ranunculaceae do tend to be less specialized than members of the “advanced” Orchidaceae or Polemoniaceae, it would be risky to conclude that lineages always evolve toward specialization (consider the many species in the “advanced” Asteraceae that appear to be generalized for pollination). It is equally risky to conclude based on taxonomy or morphology that a given flower is specialized, or what “its pollinator” is. In short, there is a distinction between *laws* and *trends*: only with the former can one argue consistently from the general to the specific. Much of what has passed for laws in pollination biology may represent trends at best.

To strengthen the empirical foundation on which we base conclusions about the fundamental nature of pollination systems—who interacts with whom, where, when, how strongly, and under what ecological circumstances—community-wide or taxon-wide studies of pollination, including the relative pollination efficiencies of different flower visitors, will be invaluable. We need careful field observation and solid natural history, with the support of experiments. And more effort in “combing” the existing literature would be well repaid.

A better understanding of pollination interactions will be very valuable for both pure and applied investigations. In what follows we support this assertion with some examples.

Some implications for ecological studies

In ecological studies we seek to understand patterns of plant (or more rarely pollinator) reproductive success across sites, seasons, and ecological contexts (presence of putative competitors or other enemies; and of direct or indirect mutualists, e.g., Waser and Real 1979), and thus to understand dynamics of populations, distributions of species, and their relative abundances in communities (Feinsinger 1978, Waser 1978, Armbruster and Herzig 1984, Kwak et al. 1991, Gathmann et al. 1994). In order to succeed we must explicitly embrace variance in interactions at different temporal scales (e.g., diurnal, seasonal, annual) and spatial scales (e.g., neighborhood, landscape, geographic), rather than describing only average interactions (see also Thompson 1994, Bronstein 1995). We must study *all* flower visitors, including those that seem "improper" based on perceived pollination syndromes. Such visitors may contribute a surprising share of plant fecundity (e.g., Motten et al. 1981, Tepedino 1981a, Waser 1979, Waser and Price 1990, Scott et al. 1993), and of interspecific interaction.

Some implications for behavioral biology

In the past few decades, behavioral biology has been revitalized by fusing traditions from ethology and psychology, by an injection of Darwinian thinking and of optimality modelling, and by input from cognitive sciences. Many empirical studies over this period have involved pollination systems, for good reasons: pollinators often are straightforward to observe and to use in experiments, and the stimuli provided by plants often can be assessed. In such work it is useful to abandon preconceived ideas about who visits whom, or about what animal group is inherently capable of what, in order to better understand information-processing and problem-solving abilities. Comparing the behaviors of very different animals (e.g., birds and bees) at similar flower-visiting tasks holds additional promise (e.g., Waser and Price 1985).

Some implications for evolutionary studies

Different flower visitors may each contribute to selection on floral traits, and a recognition of temporal and spatial variation may be more fruitful than an average, equilibrium view (e.g., Thompson 1994). Furthermore, a focus on the most obvious pollinator at a few sites and times may cause us to misinterpret past and present selection (Herrera 1995). Thus floral features that seem to be an evolutionary response to one pollinator may in fact reflect a more diverse pollination history. A similar point can be made about contributions to genetic differentiation of plants. Although pollinators are thought to foster local differentiation within plant

populations by their mostly-localized movement of pollen, there has been little success in quantitatively matching direct estimates of pollinator-mediated gene flow with spatial genetic patterns (Waser 1987, 1993, Campbell and Dooley 1992). In part this may be because some pollen-carrying visitors have been ignored. Finally, consider studies of differentiation on the scale of speciation. We urge those undertaking studies of plant hybrid zones, and other situations that provide glimpses of the speciation process, to examine all flower visitors, not only those presumed to be "correct." Acknowledging widespread opportunism and generalization reopens important questions about the contribution of pollinators to plant speciation and their role in defining plant species by influencing patterns of reproductive isolation.

Some implications for agriculture and conservation

Many of the points just raised bear on applied issues as well. For example, crop plants may interact with surrounding plants in beneficial or detrimental ways through overlap in pollinators (Free 1970). Understanding the behavioral abilities of pollinators is critical for choosing and managing them in crop situations (Parker 1981, Tepedino 1981a). And recognizing all the agents of gene flow is critical in assessing risks of crop contamination, escape of engineered genes (e.g., Klinger et al. 1992), and genetic swamping of endangered plant species (Ellstrand 1992).

There are other implications for conservation biology. A high connectance of interaction webs may influence behavior of the system following perturbation (Kevan 1991). Consider linked extinctions of plants and pollinators. Based on a preconception of specialized plant-pollinator interactions, regulatory agencies have sometimes anticipated linked extinctions where they are unlikely (e.g., Nabhan and Fleming 1993). Effort could be saved if resource managers had complete information on the interactions in pollination systems they must manage. This is *not* meant to imply that we should ignore extinctions or that generalization buffers systems from any ill effects. Indeed, generalized pollination relationships can penalize locally rare plant species through interspecific pollen transfer and other forms of competition for services of shared pollinators (Waser 1978, Campbell 1986, Kunin 1993, Petanidou et al. 1995). And generalization of pollinators need not imply resistance to perturbation, because it does not dictate generalization of plants (or vice versa). An example may be provided by the honey bee, *Apis mellifera*, which is unusual in being a super-generalist. Deliberate introductions of this species into Northern Europe, the Americas, and Australia appear in some cases to have harmed or dis-

placed native pollinators (Roubik 1978, Sugden and Pyke 1991, Evertz 1993, Paton 1993, Aizen and Feinsinger 1994). If so, the resulting pollination systems are simplified because greater specialization and reliance on honey bees has been forced on the plants. Such simplified systems may be especially vulnerable to further change.

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