

Running Head: Fenster et al., Pollination Specialization

POLLINATION SYNDROMES AND FLORAL SPECIALIZATION

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Abstract Floral evolution has often been associated with differences in pollination syndromes. Recently, this conceptual structure has been criticized on the grounds that flowers attract a broader spectrum of visitors than one might expect of their syndromes, and that flowers often seem to diverge without excluding one type of pollinator over another. Nevertheless, the larger framework surrounding pollination syndromes can be revised and extended to account more subtly for many major features of floral evolution that involve specialization onto disparate pollinators. Such evolutionary changes in specialization should be distinguished from the ecological state of specialization, which we define as the contemporary community of floral visitors. Evolutionary specialization appears to have resulted in flowers that possess functionally related complexes of traits that are maintained by stabilizing selection. Each of these traits, in turn, explains different amounts of the variation in plant-pollinator relationships. Floral rewards, in particular, are a critical locus of specialization, but flowers should be considered as complexes of floral traits co-adapted to one another. An appreciation for floral specialization should be balanced by an understanding of the limits to specialization. We hope our critique contributes to the ongoing renaissance in studies of floral adaptations.

Key words: Floral evolution; mutualism; plant-animal interaction; pollinator; pollination

INTRODUCTION

The paradigm that diverse floral phenotypes reflect specialization onto different groups of pollinators begins with Kölreuter's (1761) and Sprengel's (1793, 1996) descriptions of the interactions between plants and pollinators and the floral features that promote these interactions. Beginning with Darwin (1862), many others have elaborated on the view that floral traits reflect types of pollinators (Müller 1873, Delpino 1868-1875, Müller & Delpino 1869, Knuth 1898-1905, Baker 1963, Grant & Grant 1965, Fægri & van der Pijl 1966, Stebbins 1970, Johnson & Steiner 2000). Different pollinators promote selection for functionally different flowers, producing an array of "pollination syndromes," illustrated in Plate 1.

However, ecological data (Robertson 1928, Waser et al. 1996) seem at odds with expectations from comparative biology (Ollerton 1996, 1998), i.e., many flowers are visited by numerous animal species (Plate I). Furthermore specialization is thought to lead often to greater variance in reproductive success across years and thus ought to be selected against (Waser et al. 1996). While ecological approaches call into question the power of the pollination-syndrome concept to predict the contemporary composition of a pollinating fauna, comparative biology continues to highlight floral radiations onto different pollinators (Johnson et al. 1998, Goldblatt et al. 2001, P. Wilson, M. C. Castellanos, J. N. Hogue & J. D. Thomson, in preparation). Our goal is to reconcile these two perspectives.

In this review, we treat only evolutionary processes as they affect plants. Rather than focusing on reciprocal coevolution at or near the species level, we treat pollinators as effectively static entities to which plants sometimes adapt. The adaptations of animals to flowers (long tongues, brushes for carrying pollen, attraction to floral rewards) generally

antedate the shifts by plant lineages between different pollinators types, which concern us here.

The limited scope for reciprocal coevolution, however, does not deny an association between floral traits and types of pollinators (Schemske 1983). Rather, our perspective is that pollinators can be clustered into *functional groups* (e.g., long-tongued flies, small nectar collecting bees, etc.), behaving in similar ways on a flower and exerting similar selection pressures, which, in turn, generate correlations among floral traits (long and narrow corolla tubes, pollen presented in a certain way, particular nectar quantities and concentrations, etc.). Such pollinator-driven floral evolution can proceed with or without the animals evolving (Janzen 1980, Schemske 1983, Kiestler et al. 1984).

We define a pollination syndrome as a suite of floral traits, including rewards, which are associated with the attraction and employment of a functional group of pollinators. The floral traits are expected to be correlated with one another across plant species. However, rather than stating that “hummingbird-adapted flowers have exerted anthers and stigmas,” one can test the rule that species pollinated principally by hummingbirds tend to have more exerted anthers and stigmas than closely related species pollinated principally by moths (Thomson et al. 2000). Systematic rules remove the confounding variation in floral traits introduced by evolutionary relatedness (i.e., phylogenetic inertia; Armbruster et al. 2002).

Ollerton (1998) and Ollerton and Watts (2000) state that the predictive power of syndromes has never been tested. Indeed, the narrowly defined syndromes with detailed characterizations compiled by Fægri and van der Pijl (1966, 1971, 1979) have rarely been statistically evaluated, either with ecological data or comparative data. On the ecological front, Waser et al. (1996) suggested documenting visitation rates and the effectiveness of pollinators

for entire communities of plants and their animal visitors (see also Waser & Price 1981, 1983, Motten et al. 1981, Young 1988, Inouye et al. 1994, Gomez & Zamora 1999). While such studies quantify the current predictive power of pollination syndromes, ultimately we need to also quantify the role of visitor diversity as the selective context responsible for the origin and maintenance of floral traits. This will require postulating and testing hypotheses about the causes of selection (e.g., Waser 1983, Harder & Thomson 1989, Wilson et al. 1994, Campbell et al. 1991, Galen 1996) in a comparative context. We advocate studying both patterns of character correlation as they have arisen when plant lineages have shifted between pollinators (P. Wilson, M. C. Castellanos, J. N. Hogue & J. D. Thomson, in preparation) and the processes underlying this diversification (Armbruster 1992, 1993, Thomson et al. 2000, Thomson 2003).

We can restate the above more simply by referring to the examples of pollination syndromes in Plate 1 and asking: (1) Does the origin and maintenance of floral traits reflect differential selection exerted by different visitors? (2) What accounts for the imprecise correspondence of traits for particular syndromes; i.e., why are different floral traits expressed by various plant species with the same pollinators? Keep in mind that these cases serve to introduce the notion of pollination syndromes but may represent extremes of specialization, with the vast majority of flowers being smaller and less specialized. In the following section we provide evidence that evolutionary specialization of flowering plants for pollinators is prevalent, though to varying degrees. The rest of the review focuses on addressing the two questions posed above.

EXAMPLES OF SPECIALIZATION

Four lines of evidence suggest flowers have undergone evolutionary specialization in response to pollinators.

1. *Infraspecific pollination “ecotypes”*. These are populations that have differentiated for traits associated with pollination (Grant & Grant 1965, Miller 1981, Armbruster 1985, Pellmyr 1986, Galen 1989, Armbruster et al. 1994, Fishman & Wyatt 1999; Hansen et al. 2000). For example, spur length of *Platanthera ciliaris* orchids differs among populations in North Carolina, matching a difference in the tongue length of the primary butterfly pollinators (Robertson & Wyatt 1990). Similar correspondences have been found among closely related species of *Disa draconis*, orchids visited by long-tongued flies (Johnson & Steiner 1997), and a group of closely related species in *Diascia* (Scrophulariaceae) visited by oil-collecting bees with covarying foreleg lengths (Steiner & Whitehead 1990).

2. *Pollinator discrimination*. Pollinators selected for distinctive floral features, commonly associated with pollination syndromes, in an F₂ segregating hybrid population representing a cross between principally hummingbird-pollinated *Mimulus cardinalis* and bee-pollinated *Mimulus lewisii* (Schemske & Bradshaw 1999). In the F₂ generation, bees preferred large flowers low in anthocyanin pigments, whereas hummingbirds favored nectar-rich flowers high in anthocyanins, as would be predicted by the contemporary traits distinguishing the two species. Similarly, Campbell et al. (1997) and Meléndez-Ackerman and Campbell (1998) demonstrated that hummingbirds produced directional selection favoring traits associated with the hummingbird-pollination syndrome in a hybrid zone between red-flowered *Ipomopsis aggregata* (hummingbird syndrome) and white-flowered *I. tenuituba* (moth syndrome). These data demonstrate that pollinator preferences can select for the divergence of floral traits.

3. *Macroevolutionary studies.* Mapping floral characters and pollinators onto plant phylogenies indicates that the relationships between flowers and their pollinators are prone to parallelism and reversal (Armbruster 1992, 1993, 1996a, 1996b, Manning & Linder 1992, McDade 1992, Crisp 1994, Goldblatt & Manning 1996, Bruneau 1997, Hapeman & Inoue, 1997, Tanaka et al. 1997, Johnson et al. 1998, Baum et al. 1998, Weller et al. 1998, Johnson & Steiner 1997, Steiner 1998). Some of these evolutionary changes narrow the spectrum of pollinators. Others broaden it. Still others reflect shifts from one functional group of pollinators to another. Evolutionary specialization is readily observed in *Penstemon* (Thomson et al. 2000). Most species are pollinated by a mixture of Hymenoptera including *Bombus*, *Osmia*, *Anthophora*, and *Pseudomasaris*. Out of this moderately generalized condition, more specialized pollination by a few species of very similar hummingbirds has arisen repeatedly. In *Dalechampia*, the shift from pollination by a few species of resin-collecting bees to pollination by a variety of pollen-feeding insects in Madagascar is a clear example of the evolution of generalization (Armbruster & Baldwin 1998). Frequent transitions between pollination systems demonstrate the importance of floral specialization in the diversification of flowers.

4. *Community structure.* Several community-level studies have implicated evolutionary divergence or convergence and associated specialization in pollination in sympatric plant species (Rathcke 1983). Pollination of each plant species by a small subset of the available pollinators is a common feature of evolution in a community context (Parrish & Bazzaz 1979, Pleasants 1980, 1990, Armbruster 1986, Dilley et al. 2000). Other possible routes of specialization in pollination ecology may involve divergence in time of day that flowers open (Armbruster 1985, Stone et al. 1998), site of pollen placement (Dressler 1968,

Dodson et al. 1969, Nilsson 1987, Armbruster et al. 1994), or even convergence in floral traits resulting in Mullerian and Batesian mimicry (Schemske 1981, Nilsson 1983, respectively).

Species with floral features associated with specialized pollination often have less phenotypic variation than species with floral features associated with more generalized pollination (Fenster 1991b, Wolfe & Krstolic 1999). In addition, floral traits most closely associated with the fit between flowers and pollinators demonstrate the least phenotypic variation (Cresswell 1998). In total these data are consistent with selection acting on specialized floral systems, reducing phenotypic variation in the targets of selection.

Together, these population-, species-, phylogenetic- and community-level studies demonstrate that floral traits respond evolutionarily to differences in pollinators. Where a diversity of the pollination niches (adaptive zones) exists in space and time, natural selection has favored flowers that use one niche or another, accounting for some of the floral diversity we see today. Part of this adaptive floral diversity can be coarsely categorized into floral syndromes or characterized by systematic rules that correspond to floral syndromes.

SEMANTICS OF “SPECIALIZATION”

A plant has specialized pollination if it is successfully pollinated only by a subset of functionally grouped potential pollinators. Functional grouping refers to similarity in morphology and behavior that generates similar selective pressures (discussion by Waser et al. 1996, Armbruster et al. 1999, 2000). This similarity may reflect homology or convergence (Thomson et al. 2000). Because absolute specialization (pollination by only a single species) is extremely rare, we emphasize that specialization makes sense only as a relative measure that compares a focal population to some reference point.

Much of the literature on pollination has not distinguished between two distinct usages of the word “specialization” (Armbruster et al. 2000). *Evolutionary specialization* entails evolution to use fewer pollinators, less disparate pollinators, or a subset of pre-existing pollinators more intensively (reduced evenness). For this variable, the reference point is an ancestral population or sister-group. Specialization may have occurred even if the resulting population appears to be not very specialized. *Evolutionary specialization* implies an *evolutionary response* to differential selection pressures exerted by a subset of potential pollinators. In contrast, *ecological specialization* in pollination refers to the contemporary state of having a small number of similar species of pollinators. For this static variable, the reference point is either another contemporary population (such as a coflowering plant) or a theoretical state (such as the perfectly even use of resources embodied in most indices of niche breadth). Without a phylogenetic context, ecological specialization cannot indicate how much evolutionary specialization has occurred. Evolutionary specialization implies a decrease in the use of resource space, i.e., in the range or evenness of possible interactions between flower and pollinator, with the outcome being that pollinators are more similar to one another than if arbitrarily chosen. This contrasts with the notion of specialization strictly reflecting the number of ecological species interactions.

Failure to distinguish evolutionary and ecological specialization encourages misinterpretation. In particular, we should not reject the importance of floral specialization or floral generalization as evolutionary vectors when we find examples of intermediate ecological specialization. Perhaps most north temperate plants are visited and pollinated by a wide variety of animals, and are hence to some degree ecologically generalized. Over half of the plant species in Robertson’s (1928) community study have open radial flowers that are

apparently generalized, but this should not lead one to conclude that evolutionary changes in specialization have been unimportant in the evolutionary history of these plants. Instead, we suggest that the process of evolutionary specialization could be quite common, even though the state of narrow ecological specialization is extremely rare (see also Ollerton 1996).

Most have treated specialization in terms of the number of species that a plant uses. We advocate treating the pollinator regime in terms of functional groups of pollinators clustered by similarities in size, morphology, behavior, and *ultimately by similarity of selective pressures they exert on flowers* (Armbruster et al. 2000, P. Wilson, M. C. Castellanos, J. N. Hogue & J. D. Thomson, in preparation). Thus, many different pollinator species can belong to the same functional group. For example, *Collinsia heterophylla* might be described as generalized because it is pollinated by some 14 species of animals, yet it is more cogently viewed as specialized because the pollinators are all large-bodied, long-tongued bees in a community containing potential pollinators of much larger functional disparity (W. S. Armbruster, unpublished data). Within a species of pollinator, individuals can be divided into different functional groups. For instance, the selective pressures generated by nectar-seeking and pollen-collecting *Bombus* workers might be quite different (P. Wilson, M. C. Castellanos, J. N. Hogue & J. D. Thomson, in preparation). Functional groups, although difficult to delimit in practice, are more relevant to specialization than are species lists. Clearly, we must document not only important pollinators but also functional groupings or “pollination niches” (Beattie 1971, Armbruster et al. 1994, Gomez & Zamora 1999). In this way, the diversification of flowers can be understood adaptively, not just in terms of pollinator-species richness (a variable of more interest to insect ecologists).

Functional groupings of pollinators must be assessed by taking into account the architecture of the flower under consideration. The same pollinator (*Bombus*) may be a component of a narrow functional group pollinating specialized flowers (e.g., *Collinsia*) yet also pollinate a highly generalized flower (e.g., *Rosa*). Differences in overall structure between the two plant taxa differentially filter and focus the amount and direction of selection on floral traits. Thus, the saucer-shaped *Rosa* are pollinated by a broad taxonomic diversity of visitors that fit into the “soil and mess” pollination system typical of generalized pollination. Because pollinators move around the flower in no particular way, all visitors may be functionally equivalent. In contrast, the zygomorphic corolla of *Collinsia*, with its recessed nectaries and constricted floral tube, limits the types of visitor behavior. With such complex flowers, a large *Bombus* is not functionally equivalent to a small *Osmia*, although several species of anthophorine bees can probably be grouped with *Bombus*. As flowers become more complex, functional groups become narrower.

Pollination niches on which flowers specialize need not be related to pollinator taxonomy (although they often are). As illustration of this point, Darwin (1877) described pollination in the orchid *Herminium monorchis*, having small greenish-yellow flowers, where taxonomically very unrelated minute insects (□ 1 mm long) are compelled by the structure of the flower to behave in so similar a manner that contact of the reproductive organs are associated with the same anatomical features (the outer surface of the femur of one of the front legs) of each insect. Such insects (belonging to Hymenoptera, Diptera, and Coleoptera), are not commonly considered contributors to specialized pollination, yet the labyrinthine structure of this orchid flower imposes a uniformity of behavior and clearly fits within our notion of evolutionary specialization.

A generalized state may arise from various evolutionary dynamics. (1) Numerous animal species may pollinate equally well. (2) Selection may favor adding new pollinators without loss of old ones (e.g., Aigner 2001). (3) Selection may be averaged over episodes of selection by different pollinators (Thompson 1994, Wilson & Thomson 1996, Dilley et al. 2000). (4) Diversifying selection may be acting, but not toward flowers becoming more exclusive (Thompson 1999). The first three seem most likely, the fourth seems least likely.

Note also that flowers fitting into an ecological state of generalization are evolutionarily generalized only in the context of nearest relatives. If diverse pollinators visit a flower, but this state represents a reduction in the number of functional groups of pollinators relative to the ancestral state, then the flower is indeed more specialized evolutionarily. The identity and function of the traits contributing to this evolutionary change in niche breadth—perhaps color, fragrance, time of blooming—are of considerable interest and deserve study.

We cannot yet answer very basic questions concerning ecological and evolutionary specialization. What proportion of species with moderately generalized pollination has actually experienced evolutionary changes toward specialization? What proportion has evolved features that are referable to a pollination syndrome? Which is more common, change in the degree of pollination specialization or shifts between functional groups of pollinators? One approach to studying these issues is to map measures of specialization onto plant phylogenies (Armbruster 1992, Johnson et al. 1998, Armbruster & Baldwin 1998), thereby tracing the historical course of evolutionary specialization and generalization for each lineage. Thus, it should be possible to determine both how common evolutionary specialization really is, and how commonly it results in extreme ecological specialization. We can also address questions about the frequency of evolutionary reversals in specialization (Armbruster &

Baldwin 1998), which traits are most labile in the evolution of specialization, and how the level of specialization is maintained during shifts between classes of pollinators, e.g., from bee to butterfly (Johnson et al. 1998), from bee to beetle (Steiner 1998).

THE IMPORTANCE OF REWARDS IN FLORAL SPECIALIZATION

Not all components of syndromes (floral morphology, color, scent, reward chemistry, etc.) contribute equally to explaining variation among those animals that visit and successfully pollinate flowers (see Waser & Price 1998, Ollerton & Watts 2000). Blossom color often fares poorly in predicting pollinating visitors (McGall & Primack 1992, Armbruster 1996a, 2002, Waser et al. 1996, Waser & Price 1998) but reward chemistry and presentation do better (Simpson & Neff 1983).

Chemically diverse rewards suggest that plants have diverged in response to selection generated by the varying nutritional and reproductive preferences of pollinators (e.g., Baker & Baker 1983, 1990, Pyke & Waser 1981, Simpson & Neff 1983, Bruneau 1997). Moreover, the amount and availability of the reward may strongly limit the functional groups of pollinators attracted. For example, pollen is the reward offered by plants with poricidally dehiscent anthers (e.g., *Chamaecrista* [Caesalpinaceae], many Melastomataceae, Solanaceae, Ericaceae), but this reward is available almost exclusively to bees that can vibrate their flight muscles to buzz the flowers, while other pollen-feeding insects lack access. Similarly, long nectar tubes limit the animals that can access nectar.

Divergence in reward system usually entails evolutionary changes in specialization. Reward diversity in north-temperate regions is mostly limited to nectar and pollen, both of which are broadly attractive (except for nectar held in deep tubes and pollen held in poricidal

anthers). In the tropics and subtropics, however, there are several additional reward systems that are more restrictive in the kinds of animals they attract. (1) Oil rewards are collected by some anthophorid and melittid bees (restricted to a few genera and a few dozen species). Hundreds of tropical and subtropical plant species (and members of at least one temperate *Lysimachia*; Cane et al. 1983) are pollinated by these bees, and this specialized relationship has evolved independently many times (Simpson & Neff 1983, Buchmann 1987). (2) Fragrance is collected by male euglossine bees, apparently for olfactory displays that attract females, and pollination by these bees includes hundreds of neotropical plant species (Dressler 1982, Schemske & Lande 1984, Whitten et al. 1998) involving many independent evolutionary events (e.g., three to four times in *Dalechampia* alone; Armbruster 1993, and several times in Catasetine orchids, Chase & Hills 1992). (3) Floral resin is used in nest building by some species of bees and wasps. A resin reward is employed by several hundred species of plants occurring in most lowland tropical habitats worldwide, but has arisen only three or four times (Armbruster 1984). (4) A very specialized, but important, reward system is when flowers provide site for rearing of brood. For example, the relationship between figs and their seed-feeding wasp pollinators is extremely specialized, but involves over 900 plant species, occurring worldwide in nearly all lowland tropical forest habitats (see Wiebes 1979, Janzen 1979, Herre & West 1997, Weiblen 2002). The ecological predictive power of reward chemistry and presentation is so reliable that one hardly needs statistical testing to confirm the relationships.

It is also useful to think about using reward chemistry, fragrance chemistry, flower color, morphology, and other floral traits as both main and interactive effects in analyses of variance to explain portions of the variance in pollinators among plant species (Fægri & van

der Pijl 1966, Armbruster et al. 2000, see below section on adaptive character complexes). Much of the explainable variance is likely to be related to reward type, and certain rewards would explain more of the variance than others. Clearly the role of reward in explaining pollinator differences between flowering species and whether additional variance is explained by flower color, corolla dimensions, etc., or by trait interactions, remains to be evaluated (Ollerton & Watts 2000, J. Ollerton, personal communication). However, these patterns are likely to vary among floras around the world, and among different ecological contexts. Furthermore, different floral traits may be associated with specialization at different taxonomic scales. For example, reward is likely to be the most important component of floral trait variation to be associated with specialization on the low-level taxa of pollinators (between different bees) but other floral traits may be more important at higher taxonomic scales (e.g., flower color and degree of anther exertion may differentiate pollination by bees versus birds).

EVOLUTION IN RESPONSE TO PRINCIPAL POLLINATORS

Stebbins (1970, pp. 318-9, 1974) attempted to resolve the apparent paradox that floral diversity has arisen by divergence into pollination syndromes with the observation that flowers are visited by many species of animals (ecological generalization):

“Since selection is a quantitative process, the characteristics of the flower will be molded by those pollinators that visit it most frequently and effectively in the region where it is evolving. Hence, when an evolutionist speaks of a “bee flower” or a “hummingbird flower,” he refers to its relationship with the predominant and most

effective vector. Secondary vectors, such as *Bombus* on *Aquilegia canadensis*, may retard the process of evolutionary modification, but they are not likely either to stop it or to destroy the genetic integration of a floral type once it has evolved. Failure to recognize this principle has resulted in some unwarranted skepticism as to the action of selection by pollinators in the origin of particular forms of flowers.”

Stebbins’ use of the word “and” between “frequently” and “effectively” to us implies a multiplicative relationship: the pollinator that is both relatively most effective and relatively most frequent will usually be the most important selective force (but see Aigner 2001 for exceptions). Thus the major selective force responsible for floral evolution will be based on two components of animal activity: (1) frequency of visitation during anthesis, and (2) effectiveness of pollen transfer to appropriate stigmas on each flower visit (Grant & Grant 1965, Stebbins 1970, 1974). Most studies emphasize the former, because the presence of visitors is more easily observed and quantified than is the transfer of pollen (Waser et al., 1996, Dilley et al. 2000). Pollinator effectiveness has been quantified with a variety of metrics: the proportion of each species of visitor bearing pollen (Beattie 1971, Sugden 1986), the rate of pollen deposition on stigmas for each species (e.g., Beattie 1971, Levin & Berube 1972, Ornduff 1975, Armbruster 1985, Herrera 1987, Fenster 1991b), the number of pollen grains deposited per visit (Primack & Silander 1975, Herrera 1987), the amount of both pollen deposited on stigmas and pollen removed from anthers (Wolfe & Barrett 1988), the frequency with which each visitor species contacts anthers and stigmas (Armbruster & Herzig 1984, Armbruster 1985, 1988, 1990), fruit set per visit (Schemske & Horvitz 1984), and seed set

per visit (Parker 1981, Motten et al. 1981, McGuire & Armbruster 1991, Olsen 1997) for each species of visitor.

Many of these measures completely ignore the male component of fitness. The product of per-visit probability of contacting anthers, per-visit probability of contacting stigmas, and frequency of visitation is a useful metric of pollinator importance because it incorporates both pollen-removal and pollen-deposition components of plant reproductive success, while being relatively easy to measure in the field (Armbruster & Herzig 1984, Armbruster 1985, 1988, 1990). Leaving out the effectiveness component, incurs the risk of misidentifying the main pollinators or misconstruing a specialized system as generalized or vice versa (Hagerup 1951, Fægri & van der Pijl 1971, Stebbins 1974, Waser & Price 1981, 1983, Schemske & Horvitz 1984, Armbruster 1985, Armbruster et al. 1989, Inouye et al. 1994).

The selective importance of a pollinator species is not a constant, but depends on the other animals and plants in the community. Situation-specific effectiveness can be assessed by using simulation models to produce a “milieu analysis” (Thomson & Thomson 1992, 1998, Aigner 2001, J. D. Thomson, in preparation). These simulations require estimates of how a series of animals differ in their rates of visitation, the amount of pollen they remove in a visit, and the proportion of that pollen they deliver. One could also specify how these parameters might depend on floral characters, such as on how exerted the anthers are or how copious the flow of nectar is. From these numbers one could model the export of pollen from flowers, and thus the “quality” of the various animals. The model would yield the total number of pollen grains P that would be delivered to stigmas by a particular mixture of pollinators. Next, one could study the effects of adding one additional visit by a particular

species i of pollinator. The change in P achieved by one additional visit by pollinator species i , designated ϕP_i , is a measure of that pollinator's marginal effectiveness in the milieu under examination. By cycling through all the pollinator species and calculating ϕP_i for each, one could rank a set of co-visiting pollinators by their effectiveness. This is a Stebbinsian effectiveness in that selection acting within that particular milieu should favor characteristics that would increase the proportion of visits by the top-ranked pollinators. Selection would also favor characteristics that broadly increase the ϕP_i values of animals that visit. The evolution of features that exclude less effective pollinators may be difficult except in the radical case of transitions between major functional classes of pollinators, which likely involves direct tradeoffs.

In our view, Stebbins was correct to focus on differences in the effectiveness of pollinators, and he was correct to assert that those differences were critical to the evolution of specialization. A constructive extrapolation of these ideas is to contrast pollinators in terms of the relationship between floral characters and plant fitness, what today we would call "selection gradients" or "fitness functions". Wilson and Thomson (1996) emphasized that a precondition for specialization is that these selection gradients have differing slopes (or more generally differing shapes). Aigner (2001) has shown how floral characters might evolve to the *net* selection pressures exerted by two or more pollinators. Floral traits may evolve in response to pollinators that have the most exacting, steepest selection gradients, even when those are not the most effective (in terms of both frequency *and* effectiveness) pollinators. However these results are based on the restrictive conditions of minimal negative interactions between pollinators. When interactions are allowed, e.g., the selective gradients associated with the ancestrally most important pollinators may become much steeper as additional

pollinators are added to the system, then effective net stabilizing selection on the trait may result (Aigner 2001). Fluctuations in the pollinator milieu, and gene flow between populations with different milieus, will tend to change selection regimes and retard consistent specialization at the level of the plant species (Wilson & Thomson 1996, Waser et al. 1996, Dilley et al. 2000). Averaged over many populations, the result of this process may well be ecological generalization, even if selection for specialization is occurring each generation within each population (Thompson 1994).

Are we often misled by interpreting the commonest visitor as the most important pollinator? Only a few studies have quantified pollinator importance by the double measures of visitation frequency and effectiveness of pollen transfer. The most common visitor has frequently been found to be a poor pollinator (Armbruster 1985, Armbruster et al. 1989, Schemske & Horvitz 1984). As a result, the estimated importance of less frequent pollinators was much greater than the more common, but less effective pollinator. In terms of pollen presentation theory (Thomson et al. 2000), it is likely that the more common but less effective pollinators are parasites from the plant's point of view, in that they remove pollen that otherwise would have been transferred to stigmas by the more effective pollinators. In contrast, however, Fishbein and Venable (1996), Olsen (1997), Fenster and Dudash (2001 and C. B Fenster & M. R. Dudash, unpublished) found that the commonest visitors were also the most important pollinators.

These observations together suggest that lists of visitors, even when weighted by frequency, may give little insight into the characteristics of the main pollinators and their role as selective agents, or about the degree to which the pollination system is generalized or specialized and whether or not the flower's putative syndrome predicts its observed most

important pollinators (Waser et al. 1996). Thus, if we were to design studies comparing related plants in terms of their pollinator specialization, we need to include observations on both visitor frequencies and the rates at which each visitor type successfully transfers pollen. Furthermore, interpretation of the data would require recognition that the net effects of one particular visitor species can be strongly influenced by the composition of the rest of the visitor assemblage in any given community under study.

STUDIES REVEALING THE APTNESS OF FLORAL TRAITS

Three categories of evidence can be used to evaluate the adaptive hypothesis that specified differences among flowers are due to specialization on disparate pollinators. First, studies can focus on specific selection mechanisms, such as the determinants of pollinator effectiveness, as described in the previous section. Second, prediction of pattern using the comparative method can examine the relationship between characters and pollinators, and be tested (e.g., Armbruster 1997). Third, the way in which current selection is acting on either naturally or artificially produced variation can be examined, the topic of this section.

The following extended example will illustrate the promise and limitations associated with the study of contemporary phenotypic selection on natural variation of floral traits (see also Lande and Arnold 1983, Campbell 1989, 1996, Campbell et al. 1991, 1997, Waser 1998). Schemske and Horvitz (1984, 1989) found that Hymenoptera were the most effective pollinators (in terms of fruit set) in *Calathea ovandensis*. Of the different Hymenoptera, two relatively short-tongued species, *Rhathymus* sp. and *Bombus medius*, were the most effective pollinators. However, both were virtually absent in two of the three years of study. Even in the year they were present, they constituted only 9% of all visitors. However, only in that

year was significant phenotypic selection detected; selection favored flowers with shorter corollas, flowers better suited to pollination by short-tongued pollinators. An important conclusion from their study was that quantifying pollinator importance in terms of how much pollen is removed and deposited on stigmas on an absolute basis may not allow identification of the important selective agents acting on the flower's characteristics. Although Schemske and Horvitz demonstrated that rare pollinators can be contemporary selective agents, they did not demonstrate that short-tongued bees had been important in the origin or maintenance of the present suite of floral traits. Instead, short-tongued pollinators may act to disrupt the present suite of floral traits. Indeed, floral traits such as the long nectar tube suggest that, despite directional selection by short-tongued bees for shorter tubes, the floral morphology of *C. ovandensis* reflects selection exerted by more frequent but less effective long-tongued euglossine bees. The selection surface generated by euglossine bees on the study populations of *C. ovandensis* may actually be very flat, so shallow that fitness differences among individual plants are not detectable, revealing the limits of phenotypic selection studies when conducted only with natural phenotypic variation. We suggest this is the result of stabilizing selection averaged over the long term.

Ultimately, we would like to know to what extent and in what way pollinators have in the past selected for the character states found in plants today. Manipulative experiments can help to unravel this problem. By altering the phenotype, one may be able to re-create the variation that was eliminated by past selection. Creating this artificial, but, one hopes, realistic phenotypic variation, allows measurement of the response of pollinators in terms of visitation rates, how long they stay at flowers, whether they contact anthers and stigmas, etc. Phenotypic manipulations have long been a part of studies investigating the interaction

between floral traits and pollinators (e.g., Clements & Long 1923). The most relevant studies re-create phenotypic differences similar to those known to separate closely related species that have contrasting pollination systems, e.g., studies with the hummingbird-syndrome *Aquilegia formosa* and hawkmoth-syndrome *Aquilegia pubescens* (Fulton and Hodges 1999). In this way the effect of the manipulated character can be isolated from all the other ways in which the species differ. We will illustrate with a few studies of phenotypic manipulations that we find illuminating. Manipulating inflorescence height of the sexually deceptive orchid *Chiloglottis trilabra* (Peakall & Handel 1993), pistil height in *Brassica napus* (Creswell 2000) and degree of flower stalk bending in *Pulsatilla cernua* (Huang et al. 2002) demonstrated the optimality of the natural states, whereas natural phenotypic selection experiments might have failed to detect selection. Excision of the staminode from two bee-pollinated and two bird-pollinated *Penstemon* species demonstrated variation in function: the staminode increased pollen transfer in the bee-pollinated species, but appeared to be functionless and vestigial in the bird pollinated species (Walker-Larsen & Harder 2001). Another study manipulated the fit of *Impatiens* flowers around the bodies of bees, but found little effect on pollen transfer (Wilson 1995). Other manipulative experiments have detected directional selection on traits, e.g., nectar-spur length of Scandinavian *Platanthera* orchids by moths (Nilsson 1988), and suggest natural selection is driving populations away from the contemporary character states. However we suspect that the directional selection measured is one component of stabilizing selection, with conflicting components resulting from selection generated by pollen thieves, herbivores, allocation tradeoffs, or other factors (e.g., Armbruster 1996a). Longitudinal phenotypic selection studies that follow cohorts through time may be able to help quantify such conflicting selective pressures (Campbell 1997,

Gustaffson & Sutherland 1988).

A further advantage of phenotypic manipulation studies is that they may test hypotheses concerning the order of character evolution, if they incorporate the changes in two or more characters and the interactive effects of such changes. The approach is similar conceptually to one that geneticists have long used: knock out mutations to understand or reconstruct pathways (e.g., Beadle & Tatum 1941). Thus, we may quantify how changes in one floral trait affects pollination in the context of other changes, thus allowing the reconstruction of relative timing of key innovations. In the next section we more fully explore the role of trait interactions in the evolution of pollination specialization.

ADAPTATIVE CHARACTER COMPLEXES

In perhaps the first treatment of adaptive character complexes (“syndromes”), Simpson (1944) extended Wright’s (1931) notion of adaptive topography (fitness peaks and valleys) associated with different gene combinations to an adaptive topography associated with different combinations of phenotypic traits. In discussing floral evolution, Stebbins (1950, p. 502) stressed such a role for combinations of traits: “The flower is ... a harmonious unit,” he wrote, “an alteration of one of its parts will immediately change the selective value of modifications in all the others.” The pollination syndromes we discern as patterns of character correlation may reflect multi-trait strategies in which there are highly non-additive interactions among traits (Fenster et al. 1997). The narrow floral tubes of hummingbird-pollinated flowers may be adaptive only when anthers and stigma are strongly exerted, anther and stigma exertion may only be adaptive when nectar is copious, etc. Thus the evolution of a whole syndrome may tend to follow the origin of certain key innovations. The evolution of

nectar spurs in *Aquilegia* may have had to precede the evolution of pollination by long-tongued specialists (Hodges & Arnold 1994, 1995). The evolution of selective fruit abortion may be a key feature that predates the evolution of the mutualism between yuccas and yucca moths (Pellmyr et al. 1996, Pellmyr 1997). The evolution in *Dalechampia* of resin secretion associated with anti-herbivore defense was probably a key feature that predated the evolution of pollination by resin-collecting bees (Armbruster 1997, Armbruster et al. 1997). However, certain syndromes may tend to impede subsequent pollinator shifts, retard (or in some cases promote) subsequent speciation, and hence result in evolutionary dead-ends and be concentrated at the tips of phylogenetic branches. Clearly, a full understanding of the processes underlying the evolution of pollination syndromes requires knowledge of whether the traits that comprise a syndrome can confer higher fitness (relative to the ancestral condition) independently of each other, or whether the adaptive advantage depends on joint variation in floral features.

Few studies address the interactive value of floral traits. Comparing zygomorphic species, presumed to have more specialized pollination, with less-specialized actinomorphic species, Berg (1959, 1960) found zygomorphic taxa to have more phenotypic integration of floral traits and less correlation between floral and vegetative traits. Her results suggest that levels of covariation among floral traits respond to selection imposed by pollinators, and that there is a selective advantage associated with floral traits being intercorrelated but decoupled from variation in vegetative traits (but see Herrera 1996, Armbruster et al. 1999). Attempts to describe adaptive landscapes in floral evolution, measuring patterns of inter- and intra-specific variation, have demonstrated that certain combinations of traits, including the amount of reward, flower size, and placement of the male and female reproductive structures relative to

the reward, conferred higher fitness than alternative combinations (Armbruster 1990, Cresswell & Galen 1991). These studies also suggested that the adaptive surface of floral traits was likely to be influenced by such factors as energetic constraints on both plants and pollinators, and influenced by the physical environment (Galen 1999, Galen & Cuba 2001). Thus, we must quantify not only selection directly on floral traits, but also how the evolution of floral traits interacts with the evolution of other aspects of plant morphology and life-history, and how these are, in turn, environmentally dependent. Furthermore, quantifying selection on trait combinations may reveal selection, while doing so for any one trait, averaged across different trait combinations, may not (e.g., Armbruster 1990).

Phenotypic selection studies quantifying correlational selection may demonstrate selection for particular character combinations. Few multi-trait studies have been conducted on natural variation in syndrome characters, and they have generally been unable to detect interpretable patterns of selection acting on trait combinations (O'Connell & Johnston 1998, Maad 2000, but see Herrera 2001). If such characters are under strong stabilizing selection, there may be insufficient variation within populations for detecting selection (Fenster 1991b). Manipulative experiments that start by varying traits, one at a time, to differ from the norm of the hypothesized pollination syndrome may be more revealing. Then one can quantify interactive effects across traits comprising the syndrome, thereby testing the hypothesis that pollination is maximized by certain trait combinations (Herrera 2001). Such experiments can be conducted with different types of pollinators, quantifying the role of specific visitors in the evolution of trait combinations. Complementary effects of both color and floral morphology on nectar offerings have been demonstrated in *Ipomopsis* (Meléndez-Ackerman et al. 1997), although it is not clear whether these effects are additive or interactive.

Quantifying the interactive effects of traits may tell us more about the maintenance than the origin of syndromes (see Herrera 2001). To marshal evidence concerning the origin of syndromes, one would want to complement such experimental studies with models of the evolutionary process and with tests using comparative data.

The potentially interactive nature of floral traits may also limit our ability to detect ecological specialization. Classifying flowering-plant species according to one or a few traits (e.g., general shape, color, etc.), and asking whether there is the predicted association between these traits and pollinators, is a weak test of the ecological significance of pollination syndromes, especially if traits only confer specialization in certain combinations. We urge that multifactor approaches also be used in tests of ecological specialization.

THE ROLE OF CONSTRAINT AND CONTEXT IN THE EVOLUTION OF SPECIALIZATION

There is a wide range in the degree to which flowers are specialized. What then limits specialization, and what keeps related lineages from switching specialties? We first consider three mechanisms that may retard evolutionary change. They are not mutually exclusive, and likely reinforce one another (Schemske 1983). We next consider the role of evolutionary history in dictating the changes in specialization that do occur.

Constraints on Evolutionary Specialization:

1. Spatiotemporal fluctuation of pollinator faunas favors generalization. Herrera (1988, 1995, 1996) has provided the most complete picture of the dynamics of seasonal and site-to-site variation in pollinator visitation rates, pollinator importance, and presumably

selection. Many other studies also document spatio-temporal variation in pollinator faunas (Clements & Long 1923, Grant & Grant 1965, Bertin 1982, Schemske & Horvitz 1984, Armbruster 1985, Horvitz & Schemske 1990, Pettersson 1991, Thompson & Pellmyr 1992, Fishbein & Venable 1996, Zamora 1999, Fenster & Dudash 2001). Numerical fluctuations in the pollinator fauna may result in varying selection pressures (Schemske & Horvitz 1989, Campbell 1989; Johnston 1991, Fenster & Ritland 1994, O'Connell and Johnston 1998, Maad 2000), thus impeding specialization by converting a pollinator from a mutualist to an antagonist, and selecting for generalized pollination that would reduce variance in reproductive success (Waser et al. 1996). The benefits of specialization appear to be contradicted by highly specialized orchids that often experience unreliable pollination within a given flowering season (Calvo & Horvitz 1990), although this observation might be due to our “unstandardized” perception of pollinator reliability for a long-lived organism, i.e., because we have failed to adjust for the number of reproductive episodes or the number of seeds produced when pollination is successful.

2. Lack of appropriate genetic variation precludes evolutionary change (Bradshaw 1991). We may be observing species that have relatively recently had their pollinator communities changed from what they were during their recent evolutionary history. For example, *Dalechampia bernieri* is pollinated by tiny *Liotrigona* bees in southern Madagascar (Armbruster et al. 1993), but still retains adaptations for buzz pollination by huge carpenter bees, which pollinate this species elsewhere on the island. Either the carpenter bees vanished locally, or the plant's range changed, too recently for there to be a genetic response to selection. Adapting to another pollinator may require the appropriate genetic variation in many characters all at once, resulting in niche conservatism.

3. Evolution may be impeded by developmental and physiological genetic correlations, i.e., internal genetic homeostasis (Lerner 1954, Mayr 1963). Accordingly, syndromes are maintained by genetic correlations that evolved during a period of rapid divergence in response to selection by principal pollinators and these correlations became increasingly canalized (Stebbins 1970, 1974). Mutations leading to the disruption of any particular trait in the syndrome may have negative pleiotropic consequences, analogous to the notion that, as organisms become more complex, the potential for mutations to be deleterious increases (Fisher 1930, Orr 2000). After establishment of a syndrome, the blossom, as an integrated organ, remains static in the face of selection on particular traits by diverse pollinators (see Stebbins 1974, Ollerton 1996, Armbruster et al. 2000). Complex interactions potentially prevent genetic response to selection on floral traits, e.g., herbivores can prevent response to selection by pollinators (Herrera 2000, Gomez 2002, but see Herrera et al. 2002), and adaptive compromises arising from tradeoffs between flower size and water-use efficiency (Galen 1999, 2000).

In all three cases, stabilizing selection is the underlying mechanism. When generalization is favored because of spatiotemporal variation, selection at any moment may be directional, but it is so inconsistent that, averaged over time, selection on the whole becomes stabilizing. Inertia through a recent environmental change implies that, before the change, selection kept mutations in check and stabilized the flower to a particular phenotype. Niche conservatism involves on-going stabilizing selection either of the complex multivariate form or the simple univariate form. Canalization as a reason for stasis implies a past history of stabilizing selection (Fenster & Galloway 1997).

Studies on the genetic architecture of multi-trait syndromes are clearly needed. There are almost no such studies on floral characters — much less on ones that differ among syndromes. A recent exception focuses on the diversification of the family (Brassicaceae) into about 3000 species, almost all having two short and four long stamens. However, artificial selection on a member of the family, rapid-cycling *Brassica*, for uniform stamen height resulted in a rapid response (Karoly & Connor 2000), demonstrating that genetic variation was available. Indeed, observations that mutations can alter symmetry patterns in flowering plants (e.g., Cubas et al. 1999), that individuals can vary genetically in taxonomically conservative traits (Heuther 1968), that heritable variation exists within populations for syndrome related traits (Galen 1996) and that destabilized phenotypes can be recanalized at different states (Rendel 1967, Fenster & Galloway 1997), all argue against lack of genetic variation being the only reason why species and larger lineages are so easily characterized. Comparative approaches may indicate how traits are integrated, especially if specific sequences of character-state transitions constrain floral trait evolution. More studies are needed that quantify correlated responses to artificial selection on pollination-syndrome traits and the pleiotropic consequences of mutations affecting these traits.

Historical Contingency and Evolutionary Specialization:

While we have discussed why we suspect that evolutionary specialization is selection limited, we also anticipate that useful inferences concerning floral trait combinations exhibited by pollination syndromes can be made by considering constraints as dictating the particular trajectory of trait evolution. Thus, the contribution of constraints to the lack of universal correspondence of floral traits to particular pollination syndromes may provide greater

understanding to the observed patterns of floral variation. Floral evolution bears a strong stamp of what Williams (1992) has called “historicity,” and others “historical contingency” (Gould 1986, Futuyma 1998). We note two aspects of historicity pertinent to floral specialization.

First, there are strong phylogenetic effects on the dynamics of floral evolution. Consider the case of the clade of *Penstemon* and *Keckiella* (Scrophulariaceae, sensu lato). There are about 300 species in this clade. Parsimony suggests that there have been 14 transitions between Hymenopteran pollination and hummingbird pollination. Some of those may be reversals. Almost all species fall into these two pollination syndromes, with two likely exceptions. *Penstemon ambiguus* is thought to be principally pollinated by long-tongued *Oligodranes* flies (Straw 1963). *Penstemon tubaeflorus* is pollinated by lepidopterans as well as long-tongued bees (Clinebell & Bernhardt 1998). Flies, beetles, and Lepidoptera occasionally visit flowers of many *Penstemon* species, but evidently the clade entered an adaptive zone with two fairly narrow successful specialties, and it has only rarely left that zone. Other unrelated groups have radically different evolutionary dynamics. *Calochortus* lilies radiated in floral characters while being visited consistently by a diverse array of beetles and bees (Dilley et al. 2000). Orchid clades are notorious for specializing on particular pollinator types (Mant et al. 2002).

Second, historicity is involved in what Stebbins (1974) called “evolution along lines of least resistance” (Schluter 1996). History has limited the evolutionary ability of plants to converge on pollination syndromes from a variety of starting points. The imperfect correspondence of flowers into their syndromes reflects this historical effect and provides evidence of the course of floral evolution. Natural selection operates on pre-existing phenotypic variation, gradually changing one form to another using the structures “at hand.” The details of that pre-existing variation can both constrain adaptive evolution and stimulate

evolutionary novelty, often in ways that are not easily predicted. For example, *Silene virginica* has presumably evolved its current floral morphology in response to selection by ruby-throat hummingbirds (Fenster & Dudash 2001), but unlike most hummingbird flowers, it does not technically have a tubular corolla. Instead it is polypetalous like other Caryophyllaceae, but there is a functional tube formed by the petals being enclosed by an elongated tubular calyx. Flowers usually do not contravene their lineage (family, genus etc.) traits in response to selection towards an “ideal” combination of characters, optimal or not. At the same time, historical effects can create interesting diversity, which again disrupts the conceptual unity of syndromes. In *Dalechampia* (Euphorbiaceae), most species are bee pollinated and have showy petaloid bracts. In lineages that do not deploy anthocyanins in their foliage, the floral bracts are white or pale green. In lineages that do deploy anthocyanins in their foliage, floral bracts are pink or purple, even though the exact same pollinator species are involved (Armbruster 1996a, 2002). Either indirect selection or divergent responses to parallel selection for visible bracts has apparently increased the diversity of bract colors.

In general, historicity makes the relationship between floral traits and pollinators more complicated than one would anticipate from a naive acceptance of pollination syndromes. Clearly, a more complete understanding of the relevance of pollination specialization requires studies that examine the interaction between history, constraints, and selective response. Assessment of “systematic rules” in a phylogenetic context is one effective approach to this challenge (Thompson et al. 2000).

CONCLUSIONS

We suspect that some apparent disagreements about the importance of specialization in pollination biology are based on the struggle to deal with simplistic descriptions of specialization and pollination syndromes. A key point is the difference between the evolutionary process of specialization and the ecological state of being specialized. We suggest that, in the context of floral evolution, the evolutionary process of specialization explains much of the striking diversity of flowers. Studies of floral specialization must move from lists of pollinator species to descriptions of functional groups of pollinators and the selective pressures they exert on floral traits (Pettersson 1991). Specialized floral adaptations and syndromes are usually generated and maintained by selection created by functional groups of similar pollinators, and only rarely by single pollinator species. This should not cause us to reject the importance of specialization. Given regional variation in the composition of pollinator communities and the role of historical contingency, it is remarkable that such dynamic complexity ever converges on the traditional pollination syndromes, not that it does so incompletely.

The ecological assessment of pollination syndromes is better pursued by partitioning ecological variance into various components explained by numerous floral, animal, and environmental factors, and their possible interactions, rather than interpreting a syndrome as a fixed ecology predicted (or not) by a particular floral-trait combination. The signal in such analyses is the result of the interplay of plant response to selection generated by different groups of pollinators acting over evolutionary time, and the animals' behavioral choices and functional interactions in contemporary time.

We have cited a number of approaches to studying specialized and unspecialized pollination systems. These approaches span ecology, comparative biology, and genetics.

They include both experimental and correlational approaches. Studies to explore the role of floral-trait interactions in the origin and maintenance of pollination syndromes may also reveal much about the process underlying floral diversification. We believe that embracing a wide variety of approaches will lead to a better understanding of the role of specialization in the evolution of flowers, in all their glorious diversity.

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Figure. 1. *Penstemon strictus*, pollinated by a variety of bees (shown here) and the wasp *Pseudomasaris vespoides* and on occasion, hawkmoths who act as nectar thieves. It conforms to the bee-pollination syndrome in having purple flowers (bees also like yellow), nearly included anthers over a broad vestibule, a lower lip in the position of a landing platform, and the production of smaller amounts of concentrated nectar relative to hummingbird pollinated *P. barbatus*. 2. *Penstemon barbatus*, visited by hummingbirds and pollen-collecting bees, conforms to the hummingbird-pollination syndrome in having red flowers, exerted anthers and stigmas, a reflexed lower lip, a position that is inclined from the horizontal, and the production of copious dilute nectar. The floral tube is too long to accommodate large nectar-collecting bees. 3. *Scoliopus bigelovii*, which lives in dark moist forests and is pollinated by fungus-gnats (Mesler et al. 1980). It has lines on the sepals reminiscent of mushroom gills, and it smells like a mushroom. 4. *Ipomopsis aggregata*, visited principally by hummingbirds and conforms to the hummingbird-pollination syndrome much like *Penstemon barbatus*. If hummingbirds are absent and nectar builds up, bumblebees will also visit (Mayfield et al. 2000, Fenster & Dudash 2001, see picture 10 on plate). 5. *Ipomopsis tenuituba*, visited by hawkmoths when they are abundant and by hummingbirds (shown here), contrary to its syndrome. In keeping with the hawkmoth-pollination syndrome, it has pale pink flowers, very narrow tubes, short stamens and styles, and produces smaller amounts of nectar than *Ipomopsis aggregata*. 6. *Silene caroliniana*, ranging in color from pink to nearly white and exhibiting traits typical of the moth pollination syndrome,

including narrow corolla tubes and reduced nectar production relative to congener hummingbird pollinated *S. virginica* (9). Shown here pollinated by a hawkmoth. 7. *Dalechampia tiliifolia* being pollinated by a female *Eulaema cingulata* (Apidae: Euglossini) collecting floral resin for nest construction. 8. *Dalechampia brownsbergensis* being pollinated by male *Euglossa tridentata* (Apidae: Euglossini), which is mopping up liquid terpenoid fragrances from the stigmatic surface of a pistillate flower, substances to be used later in impressing (and seducing) females bees. Note that the resin gland is apparently absent; it is vestigial and hidden under a bractlet. 9. *Silene virginica*, pollinated by its major pollinator, hummingbird, has bright red, scentless pendant flowers that secrete copious nectar. 10. *Silene virginica* pollinated by *Bombus spp.* In one site of two studied and in one of six years of observations *Bombus spp.* was an important pollinator of *S. virginica* (Fenster & Dudash 2001). 11. *Silene stellata*, white-flowered, becomes sexually receptive in the early evening, produces relatively less nectar than hummingbird *S. virginica*, visited by moths during the night and *Bombus spp.* in the following morning (Fig. 12). 12. *Silene stellata* visited by a Noctuid moth. 13. *Salvia mohavensis*, pollinated by huge flies in the genus *Rhaphiomidas* that have tongues approximately 18 mm long.