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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 based on their syndromes and that flowers often diverge without excluding one type of pollinator in favor of another. Despite these criticisms, we show that pollination syndromes provide great utility in understanding the mechanisms of floral diversification. Our conclusions are based on the importance of organizing pollinators into functional groups according to presumed similarities in the selection pressures they exert. Furthermore, functional groups vary widely in their effectiveness as pollinators for particular plant species. Thus, although a plant may be visited by several functional groups, the relative selective pressures they exert will likely be very different. We discuss various methods of documenting selection on floral traits. Our review of the literature indicates overwhelming evidence that functional groups exert different selection pressures on floral traits. We also discuss the gaps in our knowledge of the mechanisms that underlie the evolution of pollination syndromes. In particular, we need more information about the relative importance of specific traits in pollination shifts, about what selective factors favor shifts between functional groups, about whether selection acts on traits independently or in combination, and about the role of history in pollination-syndrome evolution.

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. Darwin (1862) and many others then elaborated on the view that floral-trait combinations reflect pollinator type (Müller 1883; Delpino 1868–1875; Müller & Delpino 1869; Knuth 1906, 1908; Baker 1963; Grant & Grant 1965; Fægri & van der Pijl 1966; Stebbins 1970; Johnson & Steiner 2000). When placed in an evolutionary framework, these comparative observations suggest that different pollinators promote selection for diverse floral forms that produce an array of "pollination syndromes," (e.g., Figure 1). We define a pollination syndrome as a suite of floral traits, including rewards, associated with the attraction and utilization of a specific group of animals as pollinators. The floral traits are expected to correlate with one another across independent evolutionary events.

However, summaries of observational data show that many flowers are visited by numerous animal species (Robertson 1928; Waser et al. 1996; Ollerton 1996, 1998), which calls into question expectations from comparative biology that pollination syndromes both reflect and predict convergent selection pressures on floral traits (Fæegri & van der Pijl 1979). Furthermore, the notion that floral traits conform to a pollination syndrome and represent an adaptive response that results in specialization has been questioned because specialization is postulated to result in greater variance in reproductive success across years and, thus, ought to be selected against (Waser et al. 1996). However, comparative biology continues to highlight floral radiations onto different pollinators (Johnson et al. 1998, Goldblatt et al. 2001, Wilson et al. 2004), which likely reflects selection for specialization. How, then, can we reconcile this apparent paradox of diverse visitors at flowers with our observations of widespread convergence in floral traits?

An important first step for the study of the evolutionary relevance of pollination syndromes is to recognize that the concept implies that pollinators are clustered into functional groups (e.g., long-tongued flies or small, nectar-collecting bees) that behave in similar ways on a flower and exert similar selection pressures, which, in turn, generate correlations among floral traits (e.g., long and narrow corolla tubes, pollen presented in a certain way, or particular nectar quantities and concentrations) (Waser et al. 1996; Armbruster et al. 1999, 2000; Armbruster 2004). Such pollinator-driven floral evolution can proceed with or without the animals coevolving (Janzen 1980, Schemske 1983, Kiester et al. 1984). Here, we review the evidence that convergent selective pressures exerted by functional groups of pollinators is a prevalent underlying feature of floral diversification. We first consider the evidence for organizing diverse species of pollinators into functional groups, as well as evidence that each functional group exerts a suite of convergent selection pressures. We also evaluate whether pollinator assemblages differ in their contribution to pollination for a given plant species and, thus, may

contribute differentially to the selective pressures exerted via the reproductive success of a plant. We explore whether floral traits respond differentially to selective pressures; that is, do some traits contribute more to pollination syndromes than others? Furthermore, we consider whether floral evolution represents independent or interactive selection (i.e., correlational selection) and the consequences of each type of selection. Because we emphasize a comparative approach, we evaluate the role of historical context in shaping the contemporary patterns of floral diversity. We review the patterns of character correlation that have arisen as plant lineages have shifted between pollinators (Wilson et al. 2004) and the processes that underlie this diversification (Armbruster 1992, 1993; Thomson et al. 2000; Thomson 2003). We hope to identify areas that require further study and to better quantify the contribution of pollination syndromes to our mechanistic understanding of floral diversification.

SPECIALIZATION ONTO FUNCTIONAL GROUPS

The pollination syndrome concept implies that specialization onto functional groups is a common occurrence in plant evolution. Thus, a plant has specialized pollination if it is successfully pollinated only by a subset of functionally grouped potential pollinators; such plants are also said to occupy pollination niches (Beattie 1971, Armbruster et al. 1994, Gomez & Zamora 1999). For example, some would describe *Collinsia heterophylla* as generalized because it is pollinated by some 14 species of animals, yet it is more cogently viewed as specialized onto a functional group of large-bodied, long-tongued bees in a community that contains potential pollinators of much greater functional disparity (Armbruster et al. 2002). We further illustrate this point by reexamining Robertson's (1928) dataset from the perspective of functional groups. Summarizing Robertson's (1928) observations of 15,172 visits to 441 flowering plant species found within 10 miles of Carlinville, Illinois, Waser et al. (1996) noted that the vast majority of plants received visits by many different species of potential pollinators (see their figure 1), and they concluded that 91% of the 375 native plant taxa were visited by more than one animal species and were, therefore, somewhat generalized. Waser et al. (1996) reaffirmed this conclusion from several smaller surveys of other floras. In contrast, we follow Robertson's (1928) classification of the visitors into nine functional groups (long-tongued bees, short-tongued bees, other Hymenoptera, Diptera, Coleoptera, Lepidoptera, Hemiptera, Neuroptera, and birds) and only include animal-pollinated plant species that had frequency data of the pollinators noted. By noting frequency, we could weight the relative potential importance of the different functional classes of visitors to pollination. We arbitrarily decided that if a plant species was visited three fourths or more of the time by a single functional group, then the plant manifested specialization on that functional group. We continued to add functional groups as long as the least represented functional group visited at least one half as often as the previous most frequent functional group. Robertson (1928) also

noted which visitors were not pollinating, and we omitted these visitors from the list of pollinators for the particular plant species. In a number of cases, Robertson included frequency data in his original publications but did not do so in his 1928 book. We used the original references for the visitation frequency data [23 papers by Robertson between 1887 and 1924, 21 cited in Robertson (1928) and the others in Robertson (1923, 1924)]. In some cases, we could safely assess visitation in the absence of frequency data because some visitors did not pollinate or because only one type of visitor was observed.

Of the 278 animal-pollinated plant species for which we were able to perform quantitative evaluations, 150 species were pollinated by one functional group. Of the 85 species that were pollinated by two functional classes, 59 had pollination by two functional groups that probably exert very similar selection pressures and perhaps formed one more encompassing functional group. These cases include plants that are pollinated by (*a*) both long-tongued and short-tongued bees that likely form a pollen-collecting bee functional group (e.g., *Tradescantia* spp.); (*b*) long-tongued bees and bee flies that likely form a long-tongued, nectar-feeding insect functional group (e.g., *Agastache scrophlarieaefolia*); and (*c*) short-tongued bees and Diptera that form a small, pollen-collecting or nectar-feeding insect functional group (e.g., *Lepidium virginicum*). The dataset contains many biases, such as that caused by the vastly different effectiveness (discussed below) of the different pollinators. For example, long-tongued bees often work flowers at a much greater speed than do other visitors and, thus, are likely to contribute much more to pollination than is indicated by their census frequency alone. In all, we believe these biases lead to a conservative estimate of the number of functional groups that pollinate the Carlinville flora. Thus, we conclude that approximately 75% (209/278) of the flowering plant species exhibit specialization onto functional groups, a very different conclusion than that reached by Waser et al. (1996), who used the same data. Pollination of each plant species by a small subset of the available pollinators is common in other communities as well (Parrish & Bazzaz 1979; Pleasants 1980, 1990; Rathcke 1983; Armbruster 1986; Dilley et al. 2000). Furthermore, these subsets of pollinators often fall into functional groups in which the visitors likely share attributes of behavior, and these functional groups are predicted, on the basis of pollination syndrome traits (i.e., flower color, fragrance, reward, and morphology), in such divergent communities as a dipterocarp forest (Momose et al. 1998), an English meadow (Dicks et al. 2002), and *Costus* species in neotropical forests (Kay & Schemske 2003). We urge that investigators continue to organize pollinator communities by functional groups, and we emphasize here the need to understand more fully the degree to which such groups overlap in the selective pressures they exert on floral design (Ollerton & Watts 2000).

Functional groups, although sometimes difficult to delimit in practice, are clearly more relevant to specialization than are species lists. To regard *Silene vulgaris* as pollinated by one functional group of 26 nocturnal moths (Pettersson 1991) seems more informative than to consider it a generalist pollinated by 26 species of noctuids and sphingids. Understanding the functional relationships between the

moth species fosters further questions. Do the moths vary in their effectiveness as pollinators? (They do.) If so, why no further specialization? Functional groups permit the diversification of flowers to be understood through adaptive evolution, not just in terms of pollinator species richness. 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 homoplasy in floral traits that result in Müllerian (Schemske 1981) and Batesian mimicry (Nilsson 1983, Temeles & Kress 2003).

A number of caveats are implicit in the usage of functional groups. First, 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 that pollinates specialized zygomorphic flowers with recessed nectaries and constricted floral tubes (e.g., *Collinsia*) yet that also pollinates a highly generalized actinomorphic flower (e.g., *Rosa*) on which a broad taxonomic diversity of visitors move about in an undirected pattern. We conjecture that differences in overall structure between the two plant taxa differentially filter and focus the amount and direction of selection on floral traits. Sorting the Robertson (1928) dataset by actinomorphic versus zygomorphic flowers revealed that 52% of the 192 actinomorphic species were pollinated by one functional group, significantly less ($P < 0.01$, $\chi^2 = 11.544$) than the 61% of 86 zygomorphic species. This finding supports the notion that complex flowers reflect selection by narrower functional groups. Complexity may also lead to greater diversification rates because complexity exposes the plant to differential selective pressures exerted by different functional groups (contra Orr 2000). However, as we remark below, we have a poor comparative understanding of the types of selection pressures exerted upon plants pollinated by broad versus narrow functional groups.

Functional groups of pollinators may contain many species or only one species, and any particular species of pollinator may belong to multiple functional groups. Additionally, functional groups on which flowers specialize need not be related to pollinator taxonomy (although they often are). As an illustration of this point, Darwin (1877) described the orchid *Herminium monorchis*, which has small greenish-yellow flowers and is pollinated by taxonomically very unrelated minute insects (~1 mm long). These insects are compelled by the structure of the flower to behave in so similar a manner that contact with the plant's reproductive organs is associated with the same anatomical features (the outer surface of the femur of one of the front legs) of each insect. Such insects (members of the Hymenotpera, Diptera, and Coleoptera orders) 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 specialization onto a functional group, in this case comprising unrelated, minute insect taxa.

Generalization suggests that all pollinators are functionally equivalent (Gomez 2002). Thus, a generalized state may arise from the evolutionary dynamics of

numerous animal species pollinating equally well and selecting for the same floral features. In other words, selection may favor adding new pollinators without losing any old ones (Aigner 2001). For example, no cost is associated with nocturnally visited flowers remaining open through the following day and being visited by diurnal pollinators, as occurs in various *Silene* spp. (Pettersson 1991; R. Reynolds, C. Fenster & M. Dudash, unpublished data) and in *Burmeistera* (Muchhala 2003). In contrast, different functional groups may be exerting quite different selective pressures, and the contemporary manifestation of generalization represents an averaging of selection over many episodes by different pollinators and functional groups (Thompson 1994, Wilson & Thomson 1996, Dilley et al. 2000). Diversifying selection also may be acting simultaneously but not toward flowers becoming more exclusive (Thompson 1999). Understanding the selective pressures responsible for the maintenance (or origin, in case of reversals) of generalization seems crucial to our understanding of the mechanisms that underlie the transition from generalization to specialization. The identity and function of the traits that contribute to this evolutionary change from generalization to specialization—perhaps color, fragrance, flowering time—are of considerable interest and deserve study. We know of only a few studies that quantify selective pressures on a generalized floral design; for example, selection for larger flowers by muscoid flies on *Ranunculus acris* (Totland 2001). Comparative studies that document selection pressures and the target traits in related species with contrasting generalized and specialized pollination systems are clearly needed. Actinomorphic and zygomorphic taxa in the Boraginaceae, Solanaceae, and Lamiales, for example, may be candidate species for study (Reeves & Olmstead 2003).

EVOLUTIONARY SPECIALIZATION VERSUS ECOLOGICAL SPECIALIZATION

Although organizing pollinators into functional groups is informative, this summary only provides an assessment of ecological specialization, the contemporary state of having pollinators mainly belonging to a single functional group (Armbruster et al. 2000). 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 indexes of niche breadth). In contrast, we define evolutionary specialization as evolution toward pollination by fewer functional groups, which reflects evolution toward use of fewer pollinators, less disparate pollinators, or a change in the intensity of use of a subset of preexisting pollinators (reduced evenness). For this variable, the reference point is an ancestral population or sister group in a phylogeny. Specialization may have occurred even if the resulting population appears not to be very specialized. For example, in *Asclepias*, progressively fewer pollinators and greater specialization occur in *A. solanoana* and *A. syriaca*, subgenera of the genus that appear evolutionarily derived relative to *A. incaranata* and *A. verticillata*, which have more

generalized pollination (Kephart 1983, Kephart & Theiss 2004, Fishbein 1996). Evolutionary specialization implies an evolutionary response to differential selection pressures exerted by a subset of potential pollinators that often exert selection as functional groups.

One approach to studying these issues is to map measures of specialization onto plant phylogenies (Armbruster 1992, 1993; Johnson et al. 1998; Armbruster & Baldwin 1998; Wilson et al. 2004), thereby tracing the historical course of specialization and generalization on lineages. Thus, how common evolutionary specialization really is and how commonly it results in extreme ecological specialization can possibly be determined. 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, how the level of specialization is maintained during shifts between functional groups of pollinators, and whether evolutionary specialization is associated with floral diversification. We address these issues in a later section.

EVOLUTION IN RESPONSE TO PRINCIPAL POLLINATORS

Stebbins (1970, pp. 318–19; 1974) attempted to resolve the apparent paradox that floral diversity has arisen by divergence into pollination syndromes (evolutionary specialization) 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." Stebbins' (1970) use of the word "and" to link frequency and effectiveness implies a multiplicative relationship: The pollinator that is both relatively most effective and relatively most frequent will usually be the most important selective force. Thus, we should quantify two components of animal activity: (*a*) frequency of visitation during anthesis, and (*b*) 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 that include (*a*) the proportion of each species of visitor bearing pollen (Beattie 1971, Sugden 1986); (*b*) the rate of pollen deposition on stigmas for each species (e.g., Beattie 1971, Levin & Berube 1972, Ornduff 1975, Armbruster 1985, Herrera 1987, Fenster 1991a); (*c*) the number of pollen grains deposited per visit (Primack & Silander 1975, Herrera 1987, Waser & Price 1990, Fishbein & Venable 1996, Bingham & Orthner 1998, Gomez & Zamora 1999) and across sequential visits (Campbell 1985, Waser 1988); (*d*) the amount of pollen deposited on stigmas and pollen removed from anthers (Wolfe & Barrett 1988, Conner et al. 1995, Rush et al. 1995; Castellanos et al. 2003); (*e*) the frequency with which each visitor species contacts anthers and stigmas (Armbruster & Herzig 1984; Armbruster 1985, 1988,

1990); (*f*) 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; and (*g*) multiple components, such as pollen load, pollen removal and deposition, handling time, and potential for geitonogamy (Ivey et al. 2003). 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 and is 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).

Are we often misled by interpreting the most common visitor as the most important pollinator? The answer is frequently yes. Often, the most common visitors are poor pollinators and the least common visitors are estimated to be the best pollinators (e.g., Armbruster 1985, Armbruster et al. 1989, Schemske & Horvitz 1984, Pettersson 1991, Tandon et al. 2003). However, in other studies, the most common visitors were found to be the most important pollinators (e.g., Fishbein & Venable 1996, Olsen 1997, Fenster & Dudash 2001; and C. Fenster & M. Dudash, unpublished data).

In our view, Stebbins (1970, 1974) 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. When we examine effectiveness of different functional groups, we often observe a close match between pollinator and flower (or blossom) that is consistent with pollination syndromes. For example, hummingbirds and bees vary in their effectiveness on different *Penstemon* species (Castellanos et al. 2003), bats and hummingbirds vary in their effectiveness on alternative *Burmeistera* species, and size of bees correlates with effectiveness on *Dalehampia* taxa of different blossom sizes (Armbruster 1985, 1988, 1990). Variation in effectiveness within a functional group is frequently documented, whether we consider the group to correspond to specialization (e.g., Schemske & Horvitz 1984, 1989; Pettersson 1991; Ivey et al. 2003) or generalization (e.g., Conner et al. 1995, Rush et al. 1995).

The selective importance of a pollinator species is not a constant and likely depends on the other animals and plants in the community (Thompson 1994, 1999). In terms of pollen presentation theory (Thomson 2003), more-common but less-effective pollinators can be viewed as parasites because they remove pollen that otherwise would have been transferred to stigmas by more-effective pollinators, but this view depends critically on the specific composition of the pollinator community. Situation-specific effectiveness could, in principle, be assessed by use of simulation models to produce a "milieu analysis" (Thomson & Thomson 1992, 1998; Aigner 2001; Thomson 2003). These simulations require estimates of how a

series of animals differ in their rates of visitation, the amount of pollen they remove in each visit, and the proportion of pollen they deliver. One can also specify how these parameters might depend on floral characters, such as how exserted the anthers are or how copious the flow of nectar is. From these numbers, one can model the export of pollen from flowers and, thus, the "quality" of the various animals. The model yields the total number of pollen grains P that are delivered to stigmas by a particular mixture of pollinators. Next, one can 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 ΔP_i, is a measure of that pollinator's marginal effectiveness in the milieu under examination. By cycling through all the pollinator species and calculating ΔP_i for each, one can rank a set of covisiting pollinators by their effectiveness. This process is a Stebbinsian effectiveness in that selection acting within that particular milieu favors characteristics that increase the proportion of visits by the top-ranked pollinators and decrease visits by bottom-ranked pollinators (Castellanos et al. 2004). Selection also favors characteristics that broadly increase the ΔP_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 (Aigner 2004).

A constructive extrapolation of these ideas is to contrast functional groups in terms of the relationship between floral characters and plant fitness, what today we would call "selection gradients" or "fitness functions." Aigner (2001) has shown how floral characters might evolve to the net selection pressures exerted by two or more pollinators or functional groups. Hence, we can consider how selection pressures might differ both within and between functional groups. Floral traits may evolve in response to pollinators that have the most exacting and steepest selection gradients, even when those pollinators are not the most important pollinators (in terms of both frequency and effectiveness). However, these results are based on the restrictive conditions of minimal negative interactions between pollinators. When interactions are allowed, for example, the selective gradients associated with the ancestrally most important pollinators may become much steeper as additional pollinators are added to the system. Effective net stabilizing selection on the trait may then result (Aigner 2001). We are unaware of any studies that quantify the interaction among pollinators in terms of the selection they exert on floral traits. Clearly, further study is needed in this area.

Fluctuations in the pollinator milieu (e.g., Kephart 1983; Schemske & Horvitz 1984 1989; Horvitz & Schemske 1990; Bingham & Orthner 1998) and gene flow between populations with different milieus will change selection regimes and retard consistent specialization at the level of the plant species (Pettersson 1991, Wilson & Thomson 1996, Waser et al. 1996, Dilley et al. 2000). This development may be the reason functional groups include many functionally related species that, nonetheless, differ in the selective pressures they exert on floral traits. Averaged over many populations, the result of this process may well be a large functional group, even if selection for great ecological specialization onto one or

a few pollinators is occurring each generation within each population (Thompson 1994).

Associating effectiveness and functional groups with floral design clearly contributes to our understanding of the relevance of pollination syndromes. Functional groups provide an intuitive biological framework on which to categorize the "tangled bank" of floral visitors into groups that may vary in their effectiveness of pollination and, hence, the selective pressures they exert on plants. Ultimately, we need to focus on the interaction between selection and traits and ask the following questions: What traits do functional groups select upon? Do different functional groups select for different traits and different trait expression? We next evaluate whether the selective pressures exerted by functional groups promote specialization into categories defined by pollination syndromes.

DO POLLINATION SYNDROMES REFLECT A RESPONSE TO SELECTION BY SPECIFIC FUNCTIONAL GROUPS?

Here, we review the evidence that specialization results from convergent selection pressures exerted by functional groups of pollinators consistent with our understanding of pollination syndromes. We consider experiments based on phenotypic-selection analysis, effects of phenotypic manipulation on pollinator discrimination, covariation in floral characters and functional groups at the ecotypic level, and phylogenetic analyses testing for correspondence between shifts in trait and shifts in functional groups of pollinators.

Phenotypic Selection

The following extended example illustrates the promise and limitations of the study of contemporary phenotypic selection on natural variation of floral traits (see also Lande & Arnold 1983; Campbell 1989, 1996; Campbell et al. 1991, 1997; Waser 1998). Studies of *Calathea ovandensis* demonstrated that two relatively short-tongued Hymenoptera species, *Rhathymus* sp. and *Bombus medius*, exerted the strongest selection of all pollinators, although they were frequently absent or in low numbers (Schemske & Horvitz 1984, 1989). These pollinators exerted selection that favored flowers with shorter corolla tubes and, thus, flowers better suited to pollination by shorter-tongued pollinators. An important conclusion from the *Calathea* 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 that act on floral characteristics. Although this example demonstrates that rare pollinators can be contemporary selective agents, it does not demonstrate that short-tongued bees have 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. This finding reveals the limits of phenotypic-selection studies when such studies are conducted only with natural phenotypic variation. We suggest this finding is the result of stabilizing selection averaged over the long term.

Although many other studies have documented phenotypic selection on floral traits (reviewed in Kingsolver et al. 2001), almost all studies have focused either on general floral features, such as flower number, flower size, and display height, that are likely attractive to all functional groups (e.g., Galen 1989, Johnston 1991, Maad 2000, Totland 2001) or on traits associated with breeding systems (e.g., Fenster & Ritland 1994). Studies that specifically quantify selection on floral traits that comprise specialized pollination syndromes, in pure "parental" populations, are still rare. Campbell (1989, 1996) demonstrated that hummingbirds select for stigma exsertion and wider corollas (which allow the hummingbird to enter the corolla tube more effectively). The lack of within-population phenotypic variation for floral-syndrome traits likely has been the cause of the lack of phenotypic-selection studies on these very same traits. However, our understanding of the mechanisms of pollination-syndrome evolution would be enhanced if investigators focused in the future on studying phenotypic selection on traits that contribute to pollination syndromes so that we can assess the degree to which selection is actually convergent and whether selection is acting via male or female reproductive success, or the success of both (e.g., Campbell 1989, 1996; Johnson & Steiner 1997). We also need more phenotypic-selection studies on generalized flowers to understand the selective mechanisms that underlay their origin and maintenance. For example, large syrphid flies and sweat bees exert contrasting selection on anther exsertion in *Raphanus raphanistrum*, where other traits appear to be uniformly selected by a larger suite of pollinators (H. Sahli & J. Conner, unpublished data; see Figure 1), which suggests that the functional state of generalization may simultaneously reflect balancing and uniform selection.

Species that have floral features associated with specialized pollination often do have less phenotypic variation than species that have floral features associated with more generalized pollination (Fenster 1991b, Armbruster et al. 1999, Wolfe & Kristolic 1999). In addition, floral traits most closely associated with the fit between flowers and pollinators demonstrate the least phenotypic variation (Cresswell 1998). Such comparative data are consistent with selection acting on specialized floral systems, reducing phenotypic variation in the targets of selection, and, hence, reducing our inferential powers in contemporary phenotypic selection studies.

Unusual Phenotypic Variation

One can overcome the constraint that phenotypic-selection analysis is limited to natural levels of within-population variation by surgically modifying floral

characters to mimic between-species variation and then quantifying the relationship between character expression and aspects of pollinator activity thought to affect plant fitness (i.e., effect on visitation rate or pollen transfer) by introducing variation through manipulation (artificial or artificial selection). Another approach is to take advantage of situations in which phenotypic variation is greatly increased (hybrid zones) or can be artificially increased (by breeding programs). Thus, by examining situations in which phenotypic variation is inflated, one may possibly recreate the variation that was traversed through many generations of past selection or at least quantify the selective pressures responsible for the maintenance of a trait.

Phenotypic manipulations have long been a part of studies of the interaction between floral traits and pollinators (e.g., Clements & Long 1923). The most relevant studies recreate phenotypic differences similar to those known to separate closely related species that have contrasting pollination systems (Castellanos et al. 2004). In this way, the effect of the manipulated character can be isolated from all the other ways in which the species differ. Studies of hummingbird-pollinated *Aquilegia formosa* and hawkmoth-pollinated *Aquilegia pubescens* demonstrate that moths favor upright, white flowers, and although spur length had no effect on visitation by moths, it had a large effect on pollen removal (Fulton & Hodges 1999, Hodges et al. 2004). For *Silene* spp., hummingbirds favor large red flowers that are displayed high off the ground, whereas nocturnal moth pollinators discriminate on the basis of height alone relative to alternative trait expression found in sister species (C. Fenster, R. Reynolds & M. Dudash, unpublished data). Other examples of experimental manipulation include (*a*) inflorescence height of the sexually deceptive orchid *Chiloglottis trilabra* (Peakall & Handel 1993), (*b*) the structure of the lower lip in *Monarda didyma* (Temeles & Rankin 2000), (*c*) the flexibility of pedicels in *Impatiens capensi*s (Hurlbert et al. 1996), (*d*) pistil height in *Brassica napus* (Creswell 2000), (*e*) the addition of nectar to the nonrewarding orchid *Anacamptis morio* (Johnson et al. 2004), and (*f*) the degree of flower stalk bending in *Pulsatilla cernua* (Huang et al. 2002). These experiments demonstrate 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). A study of the manipulation of the fit of *Impatiens* flowers around the bodies of bees found little effect on pollen transfer (Wilson 1995). Other manipulative experiments have detected directional selection on traits such as nectar-spur length of Scandinavian *Platanthera* orchids by moths (Nilsson 1988) and suggest natural selection could drive populations away from the contemporary character states. However, we suspect that the directional selection measured is just one component of stabilizing selection, and conflicting components result from selection generated by pollen thieves, herbivores, allocation tradeoffs, and other factors (e.g., Armbruster 1996a). Longitudinal phenotypic selection studies that

follow cohorts through time may help quantify such conflicting selective pressures (Gustaffson & Sutherland 1988, Campbell 1997).

Trait variation may also be inflated by genetic recombination, either through controlled crosses or in natural hybrid zones. Different types of pollinators select for distinctive floral features commonly associated with pollination syndromes in an F_2-segregating hybrid population that represents a cross between principally hummingbird-pollinated *Mimulus cardinalis* and bee-pollinated *Mimulus lewisii* (Schemske & Bradshaw 1999). In the F_2 generation, bees preferred large flowers that were low in anthocyanin pigments, whereas hummingbirds favored nectar-rich flowers that were high in anthocyanins, as would be predicted by the contemporary traits that distinguish the two species. Furthermore, when flower color from one species was bred into the background of the other species, it alone seemed to result in a difference in pollinators, even while lacking covariation with nectar offerings (Bradshaw & Schemske 2003). Similarly, Campbell et al. (1997) and Meléndez-Ackerman & Campbell (1998) demonstrated that hummingbirds produce directional selection that favor traits associated with the hummingbird-pollination syndrome in a hybrid zone between red-flowered *Ipomopsis aggregata* (hummingbird syndrome) and pale-flowered *I. tenuituba* (moth syndrome). Hummingbirds selected for wide corollas (relative to the moth-pollinated species), high nectar production, and red color. Moths selected for narrower flowers but demonstrated no color preference. Preferential visitation by hummingbirds and bees to red and blue flowers, respectively, was observed in Louisiana iris hybrid zones (Wesselingh & Arnold 2000). In summary, these data demonstrate that pollinator preferences can be the source of selection for divergence of floral traits.

Comparative Data on Pollination Specialization

Associating trait shifts with shifts in functional groups is a direct test of adaptive hypotheses on which traits are selected by functional groups of pollinators. These associations can be quantified at the between-population and the among-species levels. Pollination ecotypes, populations that have genetically differentiated for traits associated with pollination (Gregory 1963–1964; Grant & Grant 1965, 1968; Breedlove 1969; Whalen 1978; Raven 1979; Miller 1981; Armbruster & Webster 1982; Armbruster 1985; Paige & Whitham 1985; Pellmyr 1986; Galen 1989; Grant & Temeles 1992; Armbruster et al. 1994; Robertson & Wyatt 1990; Johnson & Steiner 1997; Hansen et al. 2000), and floral polymorphisms within populations (Medel et al. 2003) provide strong evidence that divergent selection by different functional groups of pollinators is responsible for contemporary patterns of floral diversity within species. The lability of traits within species allows one to infer associations without necessarily taking into account ancestral and derivative relationships. If a trait such as color has diverged because of selection by one functional group (e.g., hummingbirds), then retention of a trait, even if it is an ancestral condition, is evidence that another functional group (e.g., bees) is exerting selection to maintain that trait. At the among-species level, a phylogenetic approach may

allow one to identify the direction of evolution and, thus, quantify the number of shifts to different functional groups. At this level, it is conservative to consider only derived traits and functional groups because, arguably, the retention of ancestral traits and functional pollination groups also reflects selection. Here, we take the conservative approach. Examination of traits within a framework of related ecotypes or species allows testing predictions from pollination syndromes in a specific context. Rather than stating that species pollinated by hummingbirds have exserted anthers and stigmas, we state that hummingbirds tend to pollinate species that have more exserted anthers and stigmas than do closely related species pollinated by other functional groups (Thomson et al. 2000). These systematic rules remove the confounding variation in floral traits introduced by evolutionary relatedness (i.e., phylogenetic coincidence; Armbruster et al. 2002).

In Table 1, we summarize the data on trait shifts organized by reward, morphology, color, and fragrance. The data are split into ecotypic and phylogenetic cases. Several important limitations became apparent in our literature review. Traits have not been studied uniformly; color and morphology have been investigated more often than reward and fragrance. Thus, we urge that future studies quantify the full array of traits that constitute pollination syndromes (e.g., Thomson et al. 2000).

TABLE 1 Proportions of shifts in pollinators involving four kinds of floral traits[a]

		Traits			
Shift to:		**Reward**	**Morphology**	**Color**	**Fragrance**
Bees	Ecotype	2/6 (0/2)	9/11 (2/2)	5/7 (0/2)	1/5 (0/2)
	Phylogeny	2/6 (11/11)	6/9 (10/11)	0/6 (0/11)	1/5 (3/11)
Lepidopterans: Nocturnal	Ecotype	3/4	3/4	4/4	1/2
	Phylogeny	2/4	2/5	4/4	5/5
Lepidopterans: Diurnal	Ecotype	0/1 (0/1)	0/1 (1/1)	0/1 (0/1)	1/1 (0/1)
	Phylogeny	1/2	3/3	2/3	0/2
Flies	Ecotype	0/2	3/3 (1/1)	2/3	1/2
	Phylogeny	1/1	6/7	9/9	1/9
Hummingbird	Ecotype	1/2	4/4	4/4	0/4
	Phylogeny	3/3 (0/2) (2/2)*	3/3 (2/2) (4/4)*	3/3 (0/2) (0/4)*	0/3 (0/2) (0/4)*
Bird	Phylogeny		2/2	2/2	
Beetle	Phylogeny	0/1	0/1	1/1	0/1
Mammals	Phylogeny	0/2	2/2	0/2	2/2
Total		28/52	59/72	38/69	14/59

[a]Denominators are the number of cases tallied from the literature; numerators are the number of cases that underwent a marked character change. In most cases, the shifts that are described are from one functional group to another (e.g., fly to moth, bee to bird), and in the remaining, noted within parentheses, the shifts are within functional groups (e.g., bee to bee, butterfly to butterfly). Asterisk (*) indicates a shift from Passerine to hummingbird pollination.

The ecotypic data likely reflects a severe bias because some workers may not have recorded the full list of pollinators but rather only those expected on the basis of the floral traits manifest in the plants under study (see Waser et al. 1996 for discussion). Consequently, many within-species pollinator shifts deserve further study in terms of quantifying visitors by functional groups, their effectiveness, and the divergent selection pressures they exert. Despite numerous plant phylogenetic studies that mention pollinator shifts, strikingly few map on the phylogeny actual data on both floral features and pollinators. Despite the formidable challenge in quantifying floral traits and pollinator-visitation data in a phylogenetic context, we are able to collate studies on 12 groups (Kurzweil et al. 1991; Armbruster 1992, 1993, 1996a,b; McDade 1992; Crisp 1994; Goldblatt & Manning 1996; Bruneau 1997; Hapeman & Inoue 1997; Johnson et al. 1998; Baum et al. 1998; Steiner 1998; Dilley et al. 2000; Beardsley et al. 2003; Patterson & Givinsh 2004), in addition to the 14 pollination ecotype studies. We believe the approaches used in these studies should be models for future research.

Table 1 allows us to make provisional comments on the role of functional groups in exerting convergent selective pressures on floral traits associated with pollination syndromes. Shifts in all four floral traits are associated with functional groups and often in ways that are predicted by traditional pollination syndromes. When tallied by trait, reward evolution appears to be strongly associated with shifts to hummingbird and nocturnal moth pollination (whether in terms of nectar composition or timing of nectar production); color appears to be associated with moth (to pale color), fly (to dark colors), and bird and hummingbird (to red or bright) pollination; and fragrance appears to be associated with nocturnal moth and mammal pollination and with shifts involving euglossine bees. Morphology responds consistently in all functional groups. Changes in overall flower size correspond with changes in the size of the members of the functional group, and changes in the size of the structure bearing the reward (e.g., tube or spur) tend to correspond with the size of the animals' probing structures. Most of the reward evolution in the dataset is associated with bees and reflects evolutionary specialization by *Dalechampia* spp. (Armbruster 1993) onto sundry bee-reward systems. The approximately 45 observed resin-reward species are pollinated almost exclusively by resin-collecting bees; 5 fragrance-reward species are pollinated exclusively by male euglossine bees; and 10 pollen-reward species are all pollinated by pollen-collecting bees, beetles, and flies (Armbruster 1988, Armbruster 1993, Armbruster & Baldwin 1998). Comparison of phylogenetic with ecotypic studies may allow us to determine if some traits are more labile than others and if syndrome evolution reflects particular trait order, especially if both studies can be done within the same group.

Mapping floral characters and pollinators onto plant phylogenies shows that the relationships between flowers and their pollinators are prone to parallelism and reversal (in addition to the previous citations, see Manning & Linder 1992, Tanaka et al. 1997, Weller et al. 1998). Some evolutionary changes narrow the spectrum of pollinators. For example, Calochortus lilies are pollinated by both beetles and pollen-collecting bees and exhibit ancestral floral traits, whereas species that are

pollinated by various nectaring bees manifest derived floral traits but in turn are ancestral to species pollinated by large bees (Dilley et al. 2000, Patterson & Givnish 2003). Other evolutionary changes broaden the spectrum of pollinators. For example, in the *Dalechampia* of Madagascar, a shift from pollination by resin-collecting bees to pollination by a variety of pollen-feeding insects occurs (Armbruster & Baldwin 1998). However, most of our examples reflect shifts from one functional group of pollinators to another, such as from bee to butterfly in *Disa* orchids (Johnson et al. 1998), from bee to beetle in *Ceratandra* orchids (Steiner 1998), from fly to bee and fly to moth in *Lapeirousia* (Goldblatt & Manning 1996), and from bee to hummingbird, 14 to 25 times, in *Penstemon* (Wilson et al. 2004). If most floral-trait transitions reflect shifts from one specialized functional group of pollinators to another, then we need studies that allow us to understand the adaptive significance of such shifts. Tantalizing evidence from two cases suggests that selection for increased female reproductive success may be responsible for shifts within functional groups. For example, in *Disa* orchids, selection for longer spurs by long-tongued flies occurs in populations adapted to pollination by relatively shorter-tongued flies (Johnson & Steiner 1997), and in *Platanthera* orchids, selection for increased stigmatic area results in increasing column width and transition from proboscis to eye pollination on moths (J. Maad & L. Nilsson, unpublished data). In both cases, the "ancestral" type, shorter spurs or proboscis pollination, suffers greater pollen limitation relative to the other types in specific environments. Whether we can extrapolate these results to shifts to more disparate functional groups requires future work.

Although Table 1 suggests that all traits have responded to selection by functional groups of pollinators, the various components of syndromes (e.g., floral morphology, color, fragrance, and reward chemistry) most likely do not contribute equally to explaining variation among those animals that visit and successfully pollinate flowers (see Waser & Price 1998, Ollerton & Watts 2000). For example, flower color is an important predictor at higher taxonomic levels (e.g., between bees, flies, beetles, moths, birds, and bats), although at finer taxonomic scales, it may not perform as well (e.g., between flowers that appeal to bees collecting fragrance, nectar, or pollen) (McCall & Primack 1992; Armbruster 1996a, 2002; Waser et al. 1996; Waser & Price 1998). Similarly, reward may be the most important component of floral-trait variation associated with shifts between low-level taxa of pollinators (e.g., between different functional groups of bees), but other floral traits may be more important at higher taxonomic scales (e.g., Simpson & Neff 1983, Armbruster 1984). Patterns are likely to vary among floras around the world and among different ecological contexts. Thus, use of 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 may be productive (Fægri & van der Pijl 1966, Armbruster et al. 2000, Wilson et al. 2004).

A reward's chemical composition, amount, and accessibility may strongly limit the functional groups of pollinators attracted, which suggests that plants have

diverged in response to selection generated by the varying nutritional preferences of pollinators (e.g., Baker & Baker 1983, 1990; Pyke & Waser 1981; Simpson & Neff 1983; Bruneau 1997). For example, pollen is the reward offered by plants with poricidally dehiscent anthers [e.g., *Chamaecrista* (Caesalpinaceae), many Melastomataceae, Solanaceae, and Ericaceae], but this reward is available almost exclusively to bees that can vibrate their flight muscles to buzz the flowers. Similarly, long nectar tubes limit the kinds of animals that can access nectar.

In the tropics and subtropics, several reward systems are more restrictive in the kinds of animals they attract, and each system represents many independent evolutionary events. (*a*) Oil rewards are collected by some anthophorid and melittid bees, which pollinate hundreds of tropical and subtropical plant species, as well as a few temperate species (Cane et al. 1983, Simpson & Neff 1983, Buchmann 1987). (*b*) Fragrance is collected by pollinating male euglossine bees (Dressler 1982, Schemske & Lande 1984, Chase & Hills 1992, Armbruster 1993, Whitten et al. 1998). (*c*) Plant floral resins are used in nest building by some species of bees and wasps; floral production of resin rewards has evolved three to four times among the several hundred species of resin-reward plants that grow in most lowland tropical habitats worldwide (Armbruster 1984, 1992, 1993). (*d*) Brood-rearing site is a very specialized, but important, reward system. The relationship between figs and their seed-feeding wasp pollinators involves over 900 plant species in nearly all lowland tropical forest habitats (see Wiebes 1979, Janzen 1979, Herre & West 1997, Weiblen 2002). Additional brood-site reward relationships are known in *Yucca* (e.g., Pellmyr et al. 1996), senita cacti (Flemming & Holland 1997, Holland & Flemming 1998), and *Chaemerops* palms (Dufay & Anstett 2002), and seed predators may contribute to pollination in many *Silene* species (Pettersson 1991; S. Kephart, unpublished data; R. Reynolds, C. Fenster & M. Dudash, unpublished data).

Our review of the literature reveals that functional groups differentially exert selection pressures that can account for the convergence of floral characters into pollination syndromes. Although the broad features of the evolution of pollination syndromes are confirmed, many important details that will clarify the mechanisms that underlie floral diversification remain understudied. We need greater quantification of the contribution of specific traits to pollinator discrimination, the relative lability of traits, the order in which traits evolve, and whether the order of trait evolution determines the trajectory of subsequent pollinator shifts. We address a number of these issues in the next section.

ADAPTIVE 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." Thus, patterns of character correlation may reflect highly nonadditive interactions among traits in terms of their effect on pollination success (e.g., Fenster et al. 1997). For instance, the narrow floral tubes of hummingbird-pollinated flowers may be adaptive only when anthers and stigma are strongly exserted or anther and stigma exsertion may only be adaptive when nectar is copious. (Castellanos et al. 2004). 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 antiherbivore 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 that are concentrated at the tips of phylogenic branches (Wilson et al. 2004). Clearly, a full understanding of the processes that underlie the evolution of pollination syndromes requires knowledge of whether the traits that constitute 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. Moreover, considering trait combinations may further improve predictions of functional groups by pollination syndromes.

Few studies address the interactive value of floral traits. By comparing zygomorphic species that were presumed to have more-specialized pollination and less-specialized actinomorphic species, Berg (1959, 1960) found that zygomorphic taxa had 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 a selective advantage is associated with floral traits being intercorrelated with but decoupled from variation in vegetative traits (but see Herrera 1996, Armbruster et al. 1999). Attempts to describe adaptive landscapes in floral evolution by measuring patterns of interspecific and intraspecific variation have demonstrated that certain combinations of traits, such as the amount of reward, flower size, and placement of the primary sexual organs 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 the physical environmental (Galen 1999, Galen & Cuba 2001). The ability of hummingbirds to feed at flowers of different length critically depends on the width of the flower (Temeles 1996, Temeles et al. 2002), and this dependency demonstrates that the joint consideration of traits can enhance our understanding of the precise

relationship between plant and pollinator. 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. Furthermore, quantifying selection on trait combinations may reveal adaptive mechanisms, whereas doing so for any one trait, averaged across different trait combinations, may not (e.g., Armbruster 1990).

Phenotypic selection studies that quantify correlational selection may demonstrate selection for particular character combinations. Few multitrait 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, insufficient variation may exist within populations to allow detection of selection (Fenster 1991b).

Phenotypic manipulations that vary traits, both singly and together, such that they differ from the norm of the hypothesized pollination syndrome may reveal the interactive effects among traits that constitute the syndrome, thereby testing the hypothesis that pollination is maximized by certain trait combinations (Herrera 2001). Such experiments are best done by utilizing contrasting types of pollinators (moths versus bees) to quantify the role of specific visitors in the evolution of trait combinations (Castellanos et al. 2004). Phenotypic manipulation studies may allow testing of hypotheses on the order of character evolution, if they incorporate the changes in two or more characters and the interactive effects of such changes. Alternatively, one might be able to use a genetic approach: introgress traits one or more at a time across taxa pollinated by different functional groups (Bradshaw & Schemske 2003). Therefore, we may quantify how changes in one floral trait affect pollination in the context of other changes, and, thus, allow the reconstruction of the sequence of innovations.

Very few studies quantify trait interaction effects on pollinator behavior. Complementary effects of both color and floral morphology on nectar offerings have been demonstrated in *Ipomopsis* (Meléndez-Ackerman et al. 1997), although whether these effects are additive or interactive is not clear, and the studies were all done with hummingbirds, without parallel data on hawkmoths. 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 that utilize comparative data.

HISTORICAL STARTING POINTS

We anticipate that useful inferences about 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 of the observed patterns of floral variation. Floral evolution bears a strong stamp of what has been called "historicity" (Williams 1992) or "historical contingency" (Gould 1986, Futuyma 1998).

Historicity is reminiscent of Stebbins' (1974) "evolution along lines of least resistance" (Schluter 1996). History has dictated the evolutionary ability of plants to converge on pollination syndromes from a variety of starting points. The less-than-perfect correspondence of flowers into their syndromes reflects this historical effect and provides evidence of the course of floral evolution. Natural selection operates on preexisting phenotypic variation, gradually changing one form to another by making use of the structures "at hand." The details of that preexisting 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, *S. virginica* does not technically have a tubular corolla. Instead it is polypetalous like other Caryophyllaceae, but it has a functional tube formed by the petals being enclosed by an elongated tubular calyx. Flowers usually do not contravene their lineage-specific (family-specific) traits in response to selection toward 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 same pollinator species are involved (Armbruster 1996a, 2002). Because pigmented bracts and stems appear several times simultaneously on the phylogeny, indirect selection (selection on another, genetically correlated trait, in this case, vegetative pigments) appears to have increased the diversity of bract colors (Armbruster 2002). 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 (Thomson et al. 2000).

CONCLUSIONS

We demonstrate that evolutionary specialization explains much of the striking diversity of flowers. Studies of floral specialization must continue to move from lists of pollinator species to descriptions of functional groups of pollinators and the selective pressures they exert on floral traits. Specialized floral adaptations and syndromes are often generated and maintained by selection created by functional

groups of similar pollinators, whether taxonomically related or not, and only rarely by single-pollinator species. Given regional variation in the composition of pollinator communities and the role of historical contingency, it is remarkable that such dynamic complexity often converges on the traditional pollination syndromes. We advocate the continued study of both patterns of character correlation as they have arisen when plant lineages have shifted between pollinators and the processes that underlie this floral diversification in the angiosperms.

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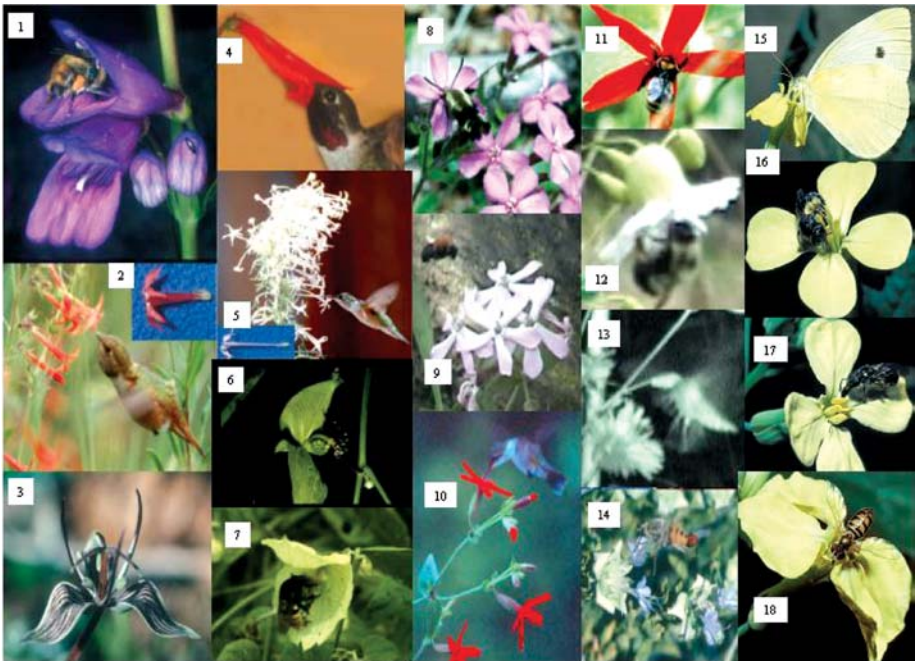

Figure 1 (1) *Penstemon strictus*, pollinated by a variety of bees (shown here) and the wasp *Pseudomasaris vespoides* and, on occasion, hawkmoths that act as nectar thieves. It conforms to the bee-pollination syndrome in having purple flowers (bees also like yellow), nearly included anthers over a broad 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* (Wilson et al. 2004). (2) *Penstemon barbatus*, visited by hummingbirds and pollen-collecting bees, conforms to the hummingbird-pollination syndrome in having red flowers, exserted anthers and stigmas, a reflexed lower lip, a position that is inclined from the horizontal, and the production of copious dilute nectar (Wilson et al. 2004). 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 accumulates, bumblebees will also visit (see pictures 10 and 11) (Mayfield et al. 2001, Fenster & Dudash 2001). (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

(*Continued*)

Figure 1 (*Continued*) flowers, very narrow tubes, short stamens and styles, and produces smaller amounts of nectar than *Ipomopsis aggregata* (Campbell et al. 1997, Melendez-Ackerman et al. 1997). (6) *Dalechampia tiliifoilia*, pollinated by a female *Eulaema cingulata* (Apidae: Euglossini), which is collecting floral resin for nest construction (Armbruster 1992). (7) *Dalechampia brownsbergensis*, pollinated by a male *Euglossa tridentata* (Apidae: Euglossini), which is mopping up liquid terpenoid fragrances from the stigmatic surface of a pistillate flower; the substances will be used later to impress (and seduce) females bees. Note that the resin gland is apparently absent; it is vestigial and hidden under a bractlet (Armbruster 1992). (8) *Silene caroliniana*, which ranges in color from pink to nearly white, presents its flowers in an upright manner and exhibits traits typical of diurnal pollination by long-tongued insects, such as narrow corolla tubes, diurnal anthesis, stigma receptivity, and reduced nectar production relative to congener hummingbird-pollinated *Silene virginica* (see picture 10) and nocturnally pollinated *Silene stellata* (see picture 13) (C. Fenster, R. Reynolds & M. Dudash, unpublished data; photograph supplied by M. Hood). Shown here pollinated by a clear-wing hawkmoth and in picture 9 by *Bombus* sp., a regular pollinator, approaching *Silene caroliniana*. The relative frequency of visitation by moths and bees to *S. caroliniana* is highly temporally variable (R. Reynolds, C. Fenster & M. Dudash, unpublished data). (10) *Silene virginica*, pollinated by its major pollinator, the hummingbird *Archilochus colubris*, has bright red, scentless flowers that are presented slightly inclined from the horizontal and that secrete copious nectar (Fenster & Dudash 2001). (11) *Silene virginica*, pollinated by *Bombus* sp. In one site of two studied and in one year of six years of observations, *Bombus* spp. were important pollinators of *S. virginica* (Fenster & Dudash 2001). (12) *Silene stellata*, white, horizontally presented flowers, becomes sexually receptive in the evening and produces relatively less nectar than hummingbird *S. virginica* or diurnally pollinated *S. caroliniana*. It is visited by nectar feeding moths during the night, of which some species also lay eggs in the flowers, and by pollen collecting *Bombus* spp., shown here the following morning (R. Reynolds, C. Fenster & M. Dudash, unpublished data).(13) *Silene stellata*, visited by a hovering Noctuid moth (R. Reynolds, C. Fenster & M. Dudash, unpublished data). (14) *Salvia mohavensis*, pollinated by huge flies in the genus *Rhaphiomidas* that have tongues approximately 18 mm long. (15–18) *Raphanus raphanistrum* exhibits traits typical of generalized pollination, including radially symmetric flowers, exposed reproductive organs and an upright flower. It is shown in picture 15 pollinated by a *Pieris* sp. collecting nectar with pollen deposited on the head and in pictures 16–18 pollinated by a halictid bee, an anthophorid bee, and a syrphid fly probing the anthers for pollen, respectively (H. Sahli & J. Conner, unpublished data).