The Scandinavian Association For Pollination Ecology Honours Knut Fægri

Published in honour of Professor Emeritus Knut Fægri in his 90th jubilee

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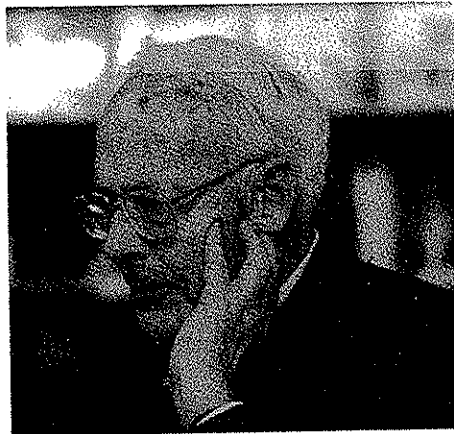
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POLLINATION "PRINCIPLES" REVISITED: SPECIALIZATION, POLLINATION SYNDROMES, AND THE EVOLUTION OF FLOWERS

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ABSTRACT: We call attention to the continuing value of the contributions of K. Fægri and L. van der Pijl in their classic book on pollination ecology (1966, 1971, 1979). We try to show that: 1) Some of the recent disagreement about the importance of specialization in the evolution of pollination systems is the result of confusing evolutionary specialization with ecological specialization. 2) Empirical and theoretical arguments about the importance of multiple pollinator species have sometimes ignored the observation that not all floral visitors are pollinators, only some of these pollinators are quantitatively important, and only a further subset generates selection. 3) Several lines of empirical evidence support the commonness of evolutionary specialization, although tight specialization in pollination ecology is extremely rare. 4) There are limits to specialization in pollination ecology and it is important to understand them. 5) If defined broadly, pollination syndromes have utility, and may reflect stable correlations among functionally related traits. The maintenance and stability of these traits may be explained by contemporary stabilizing selection, genetic/developmental constraints or homeostasis, or some combination of these processes.

INTRODUCTION

It is fitting that this volume on pollination biology is dedicated to the life-time contribution that Knut Fægri has made to our understanding of the subject. It is also appropriate that this *festschrift* will appear so close to the start of the second millennium. His book, *The Principles of Pollination Ecology*, with van der Pijl, first published in 1966, is a standard first reference for students interested in studying flower-pollinator interactions. Its clear descriptions of the floral traits associated with specific pollination modes, including a section on case histories, summarizes a wealth of natural history that has accumulated since Kölreuter's (1761), Sprengel's (1793, 1996), and Knuth's (1898-1905) early contributions. All who read the book are surely impressed at the richness and diversity of flowers and their pollinators, and also gain a better understanding of the sources of floral diversity. However, the book is more, for it deftly spans the 19th-century naturalist to the 21st-century evolutionary biologist. The book takes an adaptationist approach, emphasizing flower form as it relates to pollination function. In this way it is remarkably prescient and continues to set the direction and focus on future developments in pollination biology. Fægri and van der Pijl (1979) continually stress the importance of understanding floral diversity in the context of natural selection generating floral adaptations. By focusing on pollinators as the selective agents of floral diversity they, like Darwin (1862) and Müller (1873) before them, construct a testable paradigm. Thus we can quantify the extent to which specific pollinators are the selective agents of floral form and the

role of pollinators in generating floral diversity and maintaining trait combinations that make up pollination syndromes.

The paradigm that diversity of floral phenotype largely reflects diversity of selection by specific groups of pollinators has been recently challenged. Both new and old observations and models, cast doubt on the importance and commonness of pollination syndromes and specialization (see discussions in Waser et al., 1996; Ollerton, 1996; 1998; Waser, 1998). These include the observation that often a large number of animal species visit a single flower species and the expectation that specialization may lead to greater variance of reproductive success across years and should therefore rarely be favored (Robertson, 1928; Waser et al., 1996; Waser, 1998). Indeed there seems to be some conflict between our ecological data and our evolutionary insights (Ollerton, 1996). However, the adaptive framework posed by Fægri and van der Pijl (1979) allows for the evaluation of both issues.

Let us take as our starting definition that pollination syndromes refer to those floral traits and rewards that are associated with the attraction of specific types of pollinators. We can then quantify the actual contribution of the various visitors, predicted or not, to successful pollination. To test the predictive power of pollination syndromes, we need also a clear definition of floral adaptation to pollinators. Here we take a strictly plant-adaptation perspective: a flower fits a pollination syndrome if its pollinators fit into a category of functional similarity, e.g., similar size, shape, and behavior, ("functional groups" of pollinators). Thus we would amend any definition of pollination syndrome by stating that its origin and/or maintenance reflects selective pressures imposed by certain functional groups of similar visitors, past or present.

The importance of focusing on the adaptive significance of floral traits pertaining to functional groups of pollinators cannot be overemphasized. We suspect that some of the disagreement over the utility of pollination syndromes results from a view that syndromes indicate coevolution of

plant and pollinator species. This leads to unrealistic expectations for the predictive power of syndromes. As Waser et al. (1996) pointed out, the relationship between plants and their pollinators usually reflects "diffuse" coevolution at most (Janzen, 1980, Schemske, 1983), hence the need to focus on groups of selectively similar pollinator species. We do not think, however, that this means particular suites of floral traits are less likely to be associated with particular functional groups of pollinators, or that the rarity of coevolution calls into question the validity of pollination syndromes. We suggest instead that similar pollinators of a specific type can exert selection pressures generating suites of floral traits (pollination syndromes) with or without coevolution between plant and pollinator occurring. In other words, pollination syndromes need not reflect the reciprocal changes exerted by pairs of species that act as selective agents on each other (coevolution, *sensu stricto*; Janzen, 1980; Kiester et al., 1984). Instead, pollination syndromes simply reflect plant response to selection exerted by a pollinator type, without the plants themselves necessarily exerting reciprocal selection on the pollinators.

As a first step in quantifying whether uniform selection pressures have led to the convergent evolution of floral traits representing pollination syndromes, Waser et al. (1996) suggested valuable experimental approaches, including documenting the visitors and parameters determining their effectiveness as pollinators, e.g., pollen loads on floral visitors, rates of pollen arrival to stigmas, seed or fruit set per visit, loss of pollen, etc. (Waser and Price, 1981; 1983; Motten et al., 1981; Young, 1988; Inouye et al., 1994; Gomez and Zamora, 1999), for entire communities of plants and their animal visitors. However, because of the logistical demands of quantifying pollinator effectiveness, data collected on a community level usually comprise visitation data and/or analysis of pollen loads on the presumed vectors (e.g., Momose et al., 1998).

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in the evolution and maintenance of floral traits associated with a pollination syndrome should be tested. It is clear from many studies (e.g., Schemske and Horvitz, 1989; Herrera, 1995) that improvements in our understanding of the evolution and maintenance of pollination syndromes will need to incorporate the role of temporal and spatial variation in the importance of different pollinator species (Herrera, 1988; 1995; Thompson, 1994).

In this contribution we intend to show that most of the ideas presented by Fægri and van der Pijl (1966; 1971; 1979) concerning evolutionary specialization of plant pollination and pollination syndromes are largely valid, despite doubts voiced in the recent literature. We hope to demonstrate that: 1) Some skepticism about the importance of specialization in the evolution of pollination systems may result from confusing evolutionary specialization with ecological specialization. 2) Many empirical and theoretical arguments about the importance of multiple pollinators ignore Stebbins' (1974) useful idea about the primacy of selection by the most important class of pollinators during critical periods of evolution (see also Waser, 1998). 3) Several lines of empirical evidence support the commonness of evolutionary specialization, although tight specialization in pollination ecology is extremely rare. 4) It is important to understand and test the limits to, and reversals in, evolutionary specialization in pollination. 5) If broadly defined, pollination syndromes explain some of the variance in plant-pollinator relationships, and may often reflect stable correlations among functionally related traits; the maintenance and stability of these traits may be explained by contemporary stabilizing selection, genetic/developmental constraints or homeostasis, or some combination of these processes. To address these points we examine how visitors, pollinators, and selective agents can be distinguished from one another using examples from the literature and from our own work. We continue by reviewing the evidence for evolutionary specialization, and discussing limits to specialization. We also discuss the

importance of estimating the roles of contemporary selection versus genetic/developmental homeostasis in maintaining trait combinations associated with pollination syndromes, and conclude with suggestions for future research.

EVOLUTIONARY SPECIALIZATION VERSUS ECOLOGICAL SPECIALIZATION

In this paper we will use a simple, operational definition of specialization: successful pollination by a small number of animal species (see discussion in Waser et al., 1996; Armbruster et al., 1999). Specialization is a relative concept, because absolute specialization (e.g., pollination by one species) is extremely rare. There are two distinct aspects of specialization, and much of the literature on pollination has ignored the differences between them. We argue here that *evolutionary specialization* refers to the process of evolving in the direction of increasing specialization. In pollination, this refers to evolution from pollination by more species of animals to pollination by fewer species. Because the process of evolutionary specialization concerns the direction of evolutionary change, it does not imply starting points or end points. Hence specialization may have occurred even if the resulting population is not very specialized ecologically, or if the starting population was not especially generalized. In contrast, *ecological specialization* in pollination is a state and refers to having only a few similar species of pollinators at the present time.

Although it may sometimes be reasonable to conclude that populations with highly generalized pollination ecology have not undergone specialization, we can conclude rather little from ecological information on populations with moderately generalized pollination. It would be unwise to conclude they have not undergone specialization. Hence the distinction between *evolutionary specialization* (a process) and *ecological specialization* (a state) is critical to our understanding of specialization in pollination ecology. In our view, failure to

consider this distinction has led to confusion about the importance of evolutionary specialization in angiosperm evolution (see discussion in Ollerton, 1996). For example, consider pollination of species of *Collinsia* (Scrophulariaceae). The flowers of all species have highly modified tubular corollas, with folded, keel-like, lower petals (e.g., Kalisz et al., 1999). Because the stigma and anthers are contained in the keel, this feature restricts pollination only to bees large enough to depress the keel. Most insects that could visit more typical Scrophulariaceae flowers are denied access to the pollen. Morphological and phylogenetic analyses (Armbruster, Baldwin, and Kalisz, unpublished data) indicate that the sister group and inferred ancestor of *Collinsia* present exposed pollen in open or broadly tubular flowers. The unusual *Collinsia* floral morphology and hidden pollen appears to be the product of evolutionary specialization. Yet the list of visitors and pollinators of the flowers of *Collinsia heterophylla* at one site was surprisingly long: visitation by 17 diverse bee species, 14 of which were effective pollinators (Armbruster, unpubl. ms.). While *Collinsia heterophylla* could be viewed as having a rather generalized pollination ecology (although they are all bees; see Limits to Specialization), its appears to have evolved from more generalized ancestors and is hence evolutionarily specialized.

In this respect we are in a similar situation as community ecologists studying the role of past competition in structuring communities. To paraphrase Connell (1980), we are looking for a "ghost of specialization past," a much more challenging proposition than detecting ecological specialization. We must look behind the current ecological state and instead search for evidence of the processes that generated it. And in particular, we should not reject the importance of floral specialization as an evolutionary process just because there are few examples of extreme specialization (e.g., only one pollinator species). We agree with Waser et al. (1996) that many, probably most, temperate plants are visited and pollinated by a wide variety of animals, and are hence to some degree ecologically generalized. However, this does not lead us (nor Waser et al., 1996) to conclude that most plants have not experienced evolutionary specialization. Instead we suggest that the process of evolutionary specialization is quite common, even though the state of narrow ecological specialization is extremely rare (see also Ollerton, 1996).

This is obviously an area needing further study. What proportion of species with moderately generalized pollination have actually experienced evolutionary specialization? How can we go about studying this issue? We suggest that the most effective approach is to map measures of specialization (e.g., number of species or functional groups of pollinators) onto estimated phylogenies of groups of related plants (see Armbruster, 1992; Johnson et al., 1998; Armbruster and Baldwin, 1998). In this way one can trace the historical course of evolutionary specialization, as well as reversals to more generalized pollination, for each lineage. After sampling a reasonable number of lineages, 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 whether evolutionary specialization is reversible and at what frequency (see Armbruster and Baldwin, 1998).

FLORAL VISITORS, PRINCIPAL POLLINATORS, AND PRINCIPAL SELECTIVE AGENTS

The nature of ecological specialization observed in plant-pollinator relationships is usually highly asymmetrical. Animals usually visit and obtain food or other resources from many flower species. In contrast, flowers may be visited by few or many species of animals, but of these only a subset is likely to act as successful pollinators. Thus even the degree of ecological specialization may be difficult to determine, and flowers visited by a large number of animal species may actually be pollinated by relatively few. Furthermore, of those

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VISITORS VERSUS POLLINATORS

The function of biotic pollination systems and the selective pressures generated by pollinators are based on two components of animal activity: 1) frequency of visitation during anthesis, and 2) effectiveness of pollen pickup and transfer to stigmas by floral visitors (Grant and Grant, 1965; Stebbins, 1970; 1974; Motten et al., 1981; Waser, 1983b; Herrera, 1987; Armbruster, 1988; 1990). Most studies have emphasized the former, because the presence of visitors is more easily observed and quantified than is their transfer of pollen (see discussion in Waser et al., 1996). As Fægri and van der Pijl (1971, p. 7) and others have pointed out, however, ignoring the effectiveness component can lead to serious misunderstanding of the pollination system (e.g., misidentifying the main pollinating agent or misconstruing a specialized system as generalized, or vice versa; Hagerup, 1951; Stebbins, 1974; Waser and Price, 1981; 1983; Schemske and Horvitz, 1984; Armbruster and Herzig, 1984; Armbruster, 1985; Armbruster et al., 1989; Inouye et al., 1994).

There is general agreement on how to measure the visitation component of pollination. Presence of animals on flowers is usually easily observed, each visitor species can be counted, and relative or absolute visitation rates estimated. These can be corrected to number of visits by each species per unit time (e.g., hour, day), and per flower or blossom. For comparing among sites and species, the absolute or relative number of visits per blossom, per day of anthesis, is probably the most useful metric.

There is much less agreement on how best to estimate pollinator effectiveness (or efficacy or efficiency, as also termed; e.g., Inouye et al., 1994). Most simply, it is the number of compatible pollen grains transferred as a result of a pollinator visit. A

logical extension of this is that highest fitness accrues to plants that attract pollinators that transfer the best-quality pollen, resulting in the highest fruit and seed set, and highest offspring quality. These effects are nearly impossible to measure in the field, so all studies to date have focused on various incomplete components of pollinator effectiveness. For example Sugden (1986) noted the frequency of each species of visitor bearing pollen, an important first step. Armbruster and Herzig (1984) and Armbruster (1985; 1988; 1990) recorded the frequency that each visitor species contacted the anthers (hence probably picked up pollen) and the stigmas (and hence potentially deposited pollen). Pollinator effectiveness was calculated as the product of these two frequencies, and pollinator importance was estimated by the product of pollinator effectiveness and frequency of visitation. This is an improvement in that it incorporates both pollen-removal and deposition components of plant reproductive success, yet is feasible to measure consistently in the field (at least in plants with open blossoms). Additional steps include estimating pollinator effectiveness from rate of pollen deposition on stigmas (Armbruster, 1985; Herrera, 1987), number of pollen grains deposited on a single visit (Herrera, 1987), fruit set per visit (Schemske and Horvitz, 1994), or seed set per visit (Parker, 1981; Motten et al., 1981; McGuire and Armbruster, 1991; Olsen, 1997) for each species of visitor (see Inouye et al., 1994 for a comprehensive review of the term "pollination efficiency"). Estimating seed set is attractive because seed production is an important component of fitness. The disadvantage is that it ignores the male component of fitness, which is sometimes uncorrelated with female reproductive success (e.g., Dudash, 1991, and discussion below). In their study of the pollination of specialized *Calathea* flowers, Schemske and Horvitz (1984; 1989) considered proportional fruit set effected by each visitor species and measured the frequency at which flowers were tripped (required for both pollen pickup and deposition). They thus had indication of male and

female reproductive success. Fishbein and Venable (1996) estimated pollinium removal and insertion rates and multiplied these by visitor frequency to determine "pollinator effectiveness" (= "pollinator importance" of Armbruster, 1988; 1990; Olsen, 1997; and herein). Detailed analysis of possible fates of pollen and ovules, and a cogent terminology for its components has been presented by Inouye et al. (1994). Yet even these measures, as challenging as they are, fail to address seeds produced by animals transferring pollen in visits subsequent to the first floral visit (which is what usually is measured), or the consequences of the complex dynamics of pollinator movements among flowers.

Perhaps the best approach to understanding the relative importance of different pollinators is to use experiments. Two of us have been investigating the role of pollinators as selective agents using *Silene virginica* (Caryophyllaceae) as a model system (Fenster et al., 1996; 2000; unpublished; Dudash and Fenster, 1997; unpublished). *Silene virginica* (Caryophyllaceae) is a short-lived perennial found in eastern North America. It exhibits traits commonly associated with hummingbird pollination: bright-red, pendulous flowers, (unfused) petals forming a corolla tube, no landing platform for pollinators, no nectar guides, and copious sucrose-rich nectar. The flowers are protandrous and highly outcrossing (Dudash and Fenster, unpubl. data). We have observed no evidence of pollen limitation of female reproductive success (Dudash and Fenster, 1997), and hummingbirds appear to be efficient pollinators, transferring several times the number of pollen grains as ovules per visit (Fenster et al., 1996). We first wanted to establish the relative importance of the sole hummingbird species in eastern North America, the Ruby-throat, *Archilochus colubris*, and invertebrate visitors, syrphid flies, solitary bees, and *Bombus* spp., as pollinators of *S. virginica*. We conducted this study for five years at two sites (understory and meadow sites) near Mountain Lake Biological Station (Allegheny Mountains, Giles County; Virginia, elevation approximately 1330 m).

We chose these two sites because of the striking difference in canopy cover, which might in turn lead to different visitor faunas. To estimate the amount of female reproductive success due to hummingbirds vs. invertebrate pollinators, we randomly chose individuals to be placed into two experimental groups, caged and control. In the cage treatment, poultry-wire cages (5 x 5 cm mesh) were placed around individuals to exclude hummingbirds from visiting but allowed complete access to potential invertebrate pollinators. The control or open-pollinated treatment group were uncaged plants; this allowed complete access to all floral visitors.

In general we found that hummingbirds were the predominant pollinator of *S. virginica*, but there is considerable spatiotemporal variation in their role (Fenster and Dudash, 2000). Based on the difference in female reproductive success between the caged and control plants, across the 5 years of the study and the two sites, hummingbirds were responsible for 40 - 81% of the fruit set of control plants, 12 - 67% of the amount of seed set per fruit of control plants, and in the woodland site, 62 - 95% of the total seed of the control plants. It appears that hummingbirds are the most important pollinator of *S. virginica*, and the combination of floral traits found in *S. virginica* also suggests that hummingbirds are the primary selective agents in the evolution of floral morphology in this species. However, we have not definitively demonstrated that hummingbirds are the actual selective agents of floral form in *S. virginica*, and we discuss below our investigations to do so.

How often are we misled by interpreting the commonest visitor as the most important pollinator? In a detailed study of floral visitors to one species of plant, Armbruster et al. (1989) found that the commonest visitor to *Dalechampia magnoliifolia* (Euphorbiaceae) in Peru was *Trigona* aff. *pallens*; it visited at nearly 6.5 times the daily rate of the next most abundant visitor, *Eulaema meriana*. Although the frequency of contact with anthers was ca. 100%, frequency of contact with stigmas

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by this small bee was only about 5%. This reduced the estimated pollinator importance to less than a third of that of the rarer, but much larger *Eulaema*. In a more extensive study of 25 populations belonging to five species of *Dalechampia*, the most important pollinator was not the most abundant floral visitor in four of nine populations with multiple visitor species (Armbruster, 1985). Similarly Schemske and Horvitz (1984) observed large variation in pollinator effectiveness among visitors to *Calathea ovandensis*, a neotropical understory herb. They documented that the most frequent visitors were the least effective pollinators. In contrast, Fishbein and Venable (1996) and Olsen (1997) found that the commonest visitors were usually also the most important pollinators. These observations together suggest that lists of visitors, even when weighed by frequency, may give little insight into the characteristics of the main pollinators and their role as selective agents, a point also made by Waser et al. (1996).

Lists of visitors may also fail to tell us much about the degree to which the pollination system is generalized or specialized and whether or not pollination ecology "correctly" matches the flower's putative syndrome. For example, in the study of *D. magnoliifolia* cited above, we might have concluded from the visitor list that the pollination system was generalized (7 bee species of diverse size and behavior) and pollen served as the principal reward (collected by four of seven bee species). Our results from pollinator-importance estimates, however, indicated that pollination was specialized and fragrance was the major reward. Thus we conclude that pollination studies must include estimates of pollinator importance if they are to allow us to draw conclusions about floral adaptation and specialization.

EVOLUTION IN RESPONSE TO PRINCIPAL POLLINATORS

The value of determining pollinator frequency, effectiveness, and importance was cogently expressed by Stebbins (1974). He proposed that floral traits evolve primarily in response to the selective forces generated by the most important pollinators. With remarkable prescience of present discussions, Stebbins stated clearly the relevance of this "principle" to the role of selection and specialization in the evolution of syndromes:

"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. ... Secondary vectors ... may retard the process of evolutionary change, but they are not likely to destroy the genetic integration of the 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." (p. 62)

Several researchers have tried to operationalize Stebbins' concept by assigning primary evolutionary significance to characteristics of the pollinator(s) with highest scores in pollinator importance (as defined above; Armbruster, 1985; Herrera, 1987; Armbruster et al., 1989; Fishbein and Venable, 1996; Olsen, 1997). For example, one of us found tight covariation, across *Dalechampia* populations and species, between the size of several floral structures and the size of the principal pollinators. This suggested that plants have indeed evolved in response to selective pressures generated by principal pollinators (Armbruster, 1985; 1988; 1990). We can also attempt to quantify the role of visitors as selective agents, as we discuss below.

VISITORS VERSUS SELECTIVE AGENTS

If pollination syndromes are maintained by current selection it, should be possible to quantify the adaptive significance of floral traits in relation to the pollination syndrome. To accomplish this it will be necessary to establish the differential ability of visitors to act as selective agents on floral characters (Wilson and Thomson, 1996). In particular, to prove the utility of the pollination-syndrome concept, studies are

needed that demonstrate explicitly that pollinators associated with a particular syndrome actually select for traits associated with that syndrome. Even though particular visitors may be important pollinators, they may pollinate flowers equally with regard to variation of floral traits found in populations. These "indiscriminate" pollinators would not exert any selective pressures on those floral traits, while those that do pollinate differentially, even if less abundant, will exert selective pressures and may be responsible for the evolutionary origin and maintenance of the pollination syndrome. Note that "indiscriminate" pollination requires behavioral equivalence, both in selection of flowers (discrimination in the strict sense) and in interaction and fit with flowers. Selection may act on these traits through either male or female reproductive success or their combination.

There are several very different approaches available to quantify selection on floral features, including phenotypic selection analysis (e.g., Lande and Arnold, 1983; Campbell, 1989; Schemske and Horvitz, 1989; Campbell et al., 1991; 1997; Waser, 1998), experimental manipulation of traits (e.g., Nilsson, 1988; Peakall and Handel, 1993), as well as comparative approaches (e.g., Fenster, 1991; Armbruster, 1990; 1996a; Herrera, 1996). We need to use the full arsenal available to us in order to document the role of pollinators as selective agents in the origin and maintenance of pollination syndromes. Below we describe briefly the different techniques that can be used to quantify natural selection and what we have learned about pollinators as selective agents.

Lande and Arnold (1983) first brought to the attention of evolutionary biologists the quantitative genetic theory that allowed for straight-forward measurement of natural selection. For details see their original treatment or Endler (1986). Essentially, regression analyses can be used to reveal the relationship between a trait and the fitness of an individual. Formally, the regression analysis provides the selection gradient where fitness of an individual is regressed

on natural within-population variation for the trait. For example consider the following studies. First, Schemske and Horvitz (1984; 1989) document that the most effective pollinators of *Calathea ovandensis*, are two relatively short-tongued Hymenoptera, *Rhathymus* sp. and *Bombus medius*. However, both of these species were virtually absent in two of the three years of their study. In the one year that they were present they constituted only 9% of all visitors. However, only in this year were Schemske and Horvitz (1989) able to detect significant selection intensities such that plants producing flowers better adapted to pollination by short-tongued pollinators experienced relatively greater reproductive success. An important conclusion from their study is that quantifying pollinator importance in terms of how much pollen is removed and deposited on stigmas on an absolute basis may still lead to the misidentification of the *important selective agents* leading to, or maintaining pollination syndromes. However, while Schemske and Horvitz demonstrated that the rare pollinators are important contemporary selective agents, they did not directly demonstrate that they are either important in the evolution or maintenance of the present suite of floral traits. Instead, the selective agents identified by Schemske and Horvitz (1984) may be acting to disrupt the present suite of floral traits.

Wilson and Thompson (1996) attempted to quantify how floral traits of the native North American plants, *Erythronium grandiflorum* and *Impatiens pallida* influence the effectiveness of pollination by different sized *Bombus* pollinators. They wanted to quantify the way in which the different pollinators affect the relationship between floral morphology and reproductive success. When selection was detected in *E. grandiflorum*, all pollinators exerted selection on the trait in the same direction. Thus all the pollinators were acting to maintain the population in its pollination syndrome. In *I. pallida*, however, they found weak evidence that the different-sized pollinators exerted different selection pressures on one floral trait, suggesting that

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the different *Bombus* pollinators could lead to divergence among populations if bee frequencies were to differ among plant populations. In conclusion, these studies suggest that frequently only a subset of pollinators is responsible for floral evolution towards a pollination syndrome.

In our own work, we detect very limited phenotypic selection on floral traits in natural populations of *Silene virginica* as they relate to female reproductive success (Fenster and Dudash, unpublished). The exception is for the trait inflorescence height, which is correlated to increased female reproductive success. Because the regression analysis relies on variation present in the population, there is limited opportunity to test the effects of extreme expression of the trait, e.g., $\pm$ 2 standard deviations of the mean (by definition and assuming a normal distribution, only 5% of all individuals in the population will have traits that are > 2 standard deviations from the mean). Alternative approaches rely on phenotypic manipulation to engineer floral traits to change either singularly or in combination and to observe how reproductive success and pollinator specificity is altered. We conducted a series of manipulative studies (unpublished) that compared extreme phenotypes that differed in terms of inflorescence height, inflorescence display size, depth of the corolla tube and petal width. We were able to examine how manipulating these traits also affected male reproductive success by using fluorescent dyes which act as a good analog to pollen in this species (Fenster et al., 1996). In three of the four characters, inflorescence height, display size, and depth of corolla tube, we found that individuals expressing the trait 2 standard deviations above the normal population mean outperformed individuals in the other phenotypic classes in terms of their ability to donate pollen to other plants. This advantage was also correlated to hummingbird behavior; i.e., hummingbirds stayed longer at flowers with deeper corollas, and were more likely to visit plants with taller and larger inflorescences. This verification of the relationship between structure and function suggests that

hummingbirds have selected for these characters. Our work also demonstrates that floral-trait variation may independently affect male and female reproductive success, suggesting that assessing hermaphrodites for traits that may be targets of selection is more complex than for dioecious species (see also Campbell, 1989). We believe that a research priority should be to determine the extent to which floral trait variation reflects selection through male and/or female reproductive success.

Nilsson (1988) manipulated native *Platanthera* orchids in Scandinavia to have varying nectar spur length. He observed that trait manipulation affected both male and female reproductive success in the same direction: individuals that had shorter nectar spurs received and donated fewer pollinia. Given the length of the proboscis of the predominant hawk-moth pollinator, it is likely that the pollinator acted as a nectar thief for short spurred flowers. Peakall and Handel (1993) demonstrated that inflorescence height of the sexually deceptive orchid, *Chiloglottis trilabra,* was under selection (with trait variation affecting male and female reproductive success in the same direction). The selective optimum corresponded to the typical height from which the model, female wasps, call to attract mates.

Above we made what we think is an important distinction between contemporary selective agents, and agents that were important in the origin of the present suite of floral traits. We suggest the following experimental approach to determine whether a pollination syndrome reflects selection by the predicted pollinators. One could first manipulate one trait at a time to be different from the norm of the pollination syndrome, e.g., paint flowers blue for a red hummingbird pollinated species and compare with a red-painted control (duplicating as much as possible the appropriate floral reflectance spectra), and observe how male and female reproductive success is affected by the different visitors. In addition, one could quantify interactive effects across traits comprising the syndrome, e.g., hummingbirds may favor red flowers only

when combined with long floral tubes. Thus the role of specific visitors in the origin/maintenance of the traits can be quantified, at least if ancestral conditions can be determined from phylogenetic information.

Perhaps the first study to use a comparative approach to quantify the relationship between degree of specialization in pollination and floral traits was Berg's (1959; 1960) investigation. She demonstrated that zygomorphic species (assumed to have more specialized pollination) had greater phenotypic integration of floral traits (higher absolute correlations) and floral traits were less likely to be correlated to vegetative traits than species with actinomorphic flowers (species with less specialized pollination). Fenster (1991) demonstrated in 10 neotropical flowering species that those species with relatively longer corolla tubes (assumed to be pollinated only by long-tongued hummingbirds) had smaller proportional variance in corolla-tube length than those species with relatively shorter corolla tubes (assumed to be pollinated by both long and short tongued hummingbirds). Thus corolla-tube length was used as an *a priori* measure of specialization in pollination, with the assumption that with fewer species of pollinators (long-tube flowers) selection intensities should be greater and more consistent. This result, like Berg's before it, suggests that levels of variation and covariation of floral traits are responsive to the intensity of selection imposed by pollinators. However, more recent work (Herrera, 1996; Armbruster et al., 1999) suggests that patterns of floral morphological variation may not be easily predicted from pollination ecology. Thus each plant-pollinator association may be unique and generalizations may not be possible owing to the complex dynamics of each system.

EVIDENCE SUPPORTING COMMONNESS OF EVOLUTIONARY SPECIALIZATION

There are at least three lines of circumstantial evidence suggesting that evolutionary specialization of pollination systems is reasonably common: 1) pollination systems and floral morphology associated with pollination are often evolutionarily labile at the interspecific level, 2) genetically based among-population (within species) variation in pollination ecology (pollination ecotypes) is often observed, and 3) community-level floral character displacement may be fairly common.

Recent studies in which floral characters and pollinators are mapped onto independently derived plant phylogenies show largely that the relationships between flowers and their pollinators are evolutionarily labile and prone to parallelism and evolutionary reversal (Armbruster, 1992; 1993; 1996a; 1996b; Manning and Linder, 1992; Goldblatt and Manning, 1996; Bruneau, 1997; Hapeman and Inoue, 1997; Tanaka et al., 1997; Johnson et al., 1998; Baum et al., 1998; Weller et al., 1998). These changes can affect both morphological and biochemical components of the pollination system (e.g., Armbruster, 1993). Not all of these evolutionary changes reflect specialization, however, as when there is a shift from pollination by one pollinator species to pollination by another, or when there is a shift from few pollinator species to pollination by a larger number (evolutionary generalization; see below). Nevertheless, much of the observed evolutionary change is specialization (i.e., evolution in the direction of decreasing number of pollinator species, as explained above).

Observations of reversal from specialized to generalized pollination suggest that strong consistent selection pressures may maintain specialized syndromes. For example, pollination of short-, straight-tube species of *Aphelandra* (Acanthaceae) by a variety of short-billed hummingbird species is a derived condition, while pollination of longer- curve-tube species by one or two hermit hummingbird species is the ancestral condition (McDade, 1992). The shift in *Dalechampia*, from pollination by few species of resin-collecting bees to pollination by a variety of pollen feeding insects in Madagascar is another clear example of loss of specialization (Armbruster and Baldwin, 1998). Finally, most mem-

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bers of the derived plant family Asteraceae have floral features promoting pollination by a wide range of insects (Waser et al., 1996); this family has presumably evolved from ancestors with more specialized pollination (Soltis et al., 1997; Donoghue et al., 1998; Doyle, 1998; Nandi et al., 1998; Soltis et al., 1999). The variety of floral visitors to many flowers suggests that selective agents for diversification are ever-present, since each visitor has the potential to be dominant pollinators if the biotic environment changes (Baker, 1963; Stebbins, 1974). Frequent transitions between pollination systems also suggest the importance of consistent directional selection in the evolution of pollination syndromes.

Evolutionary specialization has also been observed at the infraspecific level as demonstrated by studies of pollination ecotypes (genetic differentiation in floral traits associated with pollination; Grant and Grant, 1965; Miller, 1981; Armbruster, 1985; Pellmyr, 1986; Galen, 1989; Robertson and Wyatt, 1990; Steiner and Whitehead, 1990; Armbruster et al., 1994; Johnson and Steiner, 1997). Several studies are particularly worth describing. Robertson and Wyatt (1990) demonstrated that spur length of the *Platanthera* orchid varies regionally and covaries with the proboscis length of the predominant pollinator. A similar pattern was suggested by Johnson and Steiner (1997) for nectar spur length in south African *Disa* orchids. Steiner and Whitehead (1990) showed regional co-variation of floral spur length in a *Diascia* species (Scrophulariacae) and the fore-leg length of one species of pollinating *Rediviva* (Melittidae) in South Africa. Perhaps the most dramatic, though largely unconfirmed, example of infraspecific specialization in pollination is the Grants' (1965) work with *Gilia splendens* in California, where the species has apparently differentiated into hummingbird, bee-fly (Bombyliidae), cyrtid-fly (Cyrtidae), and autogamous pollination ecotypes (races).

Several community-level studies have implicated evolutionary divergence in pollination ecology by sympatric plant species (i.e., community-wide floral character dis-

placement; Pleasants, 1980; 1990; Rathcke, 1983; Armbruster, 1986). Some studies indicate that evolutionary specialization on different species of pollinators has occurred and may be a common part of evolution in a community context (Parrish and Bazzaz, 1979; Pleasants, 1980; 1990; Armbruster, 1986). Similarly, evolutionary "organization" of flowering seasons also indicates increasing specialization in pollination (see review in Rathke, 1983; cf. also Kochmer and Handel, 1986). Other possible routes of specialization (in the broadest sense) in pollination ecology may involve divergence in time of day of flowering (Armbruster, 1985; Stone et al., 1998), or site of pollen placement (Dressler, 1968; Nilsson, 1987; Armbruster et al., 1994). However, because these routes of specialization do not necessarily involve decreasing the diversity of pollinators (as used in our working definition of specialization), we will not consider them further here. In sum, these phylogenetic-, population-, and community-level studies demonstrate that floral traits are evolutionarily labile, can respond rapidly to selection by pollinators, and often, but not always, evolve in the direction of specialization.

LIMITS TO SPECIALIZATION

Not all plant taxa demonstrate obvious radiations in floral morphology and pollination; e.g., compare composites with orchids. What limits specialization in these groups and/or regions? Here we touch briefly upon a number of ecological, genetic, and developmental phenomena, which may limit the ability of plants to respond to selective pressures, reducing the opportunity for the origin of specialized pollination. Perhaps one of the most intuitively appealing counter-arguments to specialization is the spatio-temporal fluctuation of pollinator faunas. 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. His argument and those of others (e.g., Waser et al., 1996) seem

quite reasonable: fluctuating selective pressures impede adaptation and the evolution of specialization (but cf. Stebbins 1974, p. 62). Furthermore, fluctuation of the pollinator fauna will instead select for reduced variance in reproductive success and hence generalized pollination systems (Waser et al., 1996). Indeed, Herrera's observations corresponds to Fenster's and Dudash's work described above and to results of other studies that document important temporal and spatial variation in the composition of pollinators visiting particular plant species (Bertin, 1982; Schemske and Horvitz, 1984; Armbruster, 1985; Horvitz and Schemske, 1990; Pettersson, 1991; Thompson and Pellmyr, 1992; Fishbein and Venable, 1996). In sum, these results suggest that the role pollinators play as selective agents may be context dependent, i.e., influenced by the composition of the pollinator community found in a given population of the focal plant species (Thompson, 1994), and the intensity and even direction of selection on individuals with different floral morphologies may also vary temporally and spatially. Indeed, varying selection pressures appear to be characteristic of studies quantifying selection on floral traits (Schemske and Horvitz, 1989; Campbell, 1989; Johnston, 1991; Fenster and Ritland, 1994; O'Connell and Johnston, 1998).

The degree of variance in the composition of the pollinator fauna may be strongly environmentally dependent, and may, as we argue above, introduce a bias into the data. Many studies have been conducted in northern temperate, alpine, and arctic ecosystems, which may shift our impressions toward the importance of generalization (see papers reviewed by Waser et al., 1996; and herein). Clearly more community-wide studies are needed that both compare spatial and temporal variation in pollinators across ecosystems and quantify the degree of pollinator specialization. Another approach would be to measure the variance of reproductive success, perhaps measured as the degree of pollen limitation, in specialists versus their closely related sister groups. These studies also have an imperative given human induced disturbance of natural ecosystems which may result in increased variance of composition of native pollinator fauna (see Rathcke and Jules, 1993; Aizen and Feinsinger 1994a; 1994b).

Another apparent limit to specialization in pollination ecology is imposed by plants being able to specialize only on *groups* of pollinators that generate similar selective pressures. This means that it is unlikely for a plant to specialize on a single pollinator species if there are other species present that have similar behavior and interaction ("fit") with floral parts. This may lead to confusion about the degree of ecological specialization actually expressed by a plant species. For example, a species like *Collinsia heterophylla*, described above, may appear generalized because it is pollinated by some 14 species of visitors, yet be more appropriately considered specialized because the pollinators are all fairly similar bees of medium to large size.

EVOLUTION OF POLLINATION SYNDROMES

Fægri and van der Pijl (1966; 1971; 1979) made major contributions towards defining pollination syndromes. Although their classification of syndromes may be a little finer and more deterministic than we are comfortable with today, they were careful to caution students of pollination biology against hasty application of syndromes to plants about which too little was known. Most significantly, they related flower form to pollination function and related floral chemistry and color to pollinator attraction, placing emphasis on the material basis of attraction (e.g., rewards and advertisements) and the physical basis of pollination (e.g., attributes determining precision of pollen placement and pollinator "fit" in flowers). Our interest in pollination syndromes has centered on the selective forces that are responsible for the origin and maintenance of the defining features of the syndromes. How have so many floral traits come to covary, and why is there so much convergence (see Ollerton, this volume)? Other authors (e.g., Ollerton, this volume) have focused on the predictive value of

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pollination syndromes. Pollination syndromes, if defined very broadly, do have significant predictive power (see below). However, not all components of the classic syndromes (e.g., color, scent, reward chemistry) contribute equally to explaining variation in what animals are attracted, visit, and successfully pollinate (see Waser and Price, 1998).

The material basis of pollinator attraction is probably the most robust component of the pollination syndrome. This comprises the 1) reward (or "primary attractant"), which is the ultimate motivation for an animal visiting the flower (usually food) and 2) the advertisements (or "secondary attractants"), which are the cues provided by the plant to promote associative learning by the pollinator. The chemistry of the reward and advertisements without doubt determines the assemblage of animals that visit the flower (Simpson and Neff, 1983). This results in some degree of ecological specialization in terms of which animals are attracted, depending especially on what reward is produced. The variation in the chemistry of rewards seen across species also suggests plants have evolved in response to selection generated by the nutritional and reproductive needs of pollinators (e.g., Simpson and Neff, 1983; Baker and Baker, 1983; 1990), although the contributing roles of biochemical coincidences and exaptation should not be ignored (Armbruster 1993; 1996b; 1997). Thus plants have undergone evolutionary specialization in response to the selective pressures generated by foraging animals.

Reward diversity in the temperate zone is relatively limited. The major rewards are nectar and pollen, both of which are attractive to large numbers of animal species. Hence working in the temperate and arctic zones, one gets the impression that specialization through reward chemistry is rare. In the tropics and subtropics, however, there are several additional reward systems, which themselves are quite restrictive in the kinds of animals they attract. Oil rewards are collected by a few genera of anthophorid and melittid bees for provisioning of larvae. Although only a

few genera and a several dozen species of bees collect oils, hundreds of tropical and subtropical plant species are pollinated in this way, and the relationship has evolved independently many times (Simpson and Neff, 1983). Another specialized reward system, involving hundreds of neotropical plant species, is production of fragrances collected by male euglossine bees. The bees collect fragrances from flowers and other sources apparently for olfactory displays involved in attracting females (Dressler, 1982; D. Roubik and W. M. Whitten, pers. comm.). This syndrome has evolved independently dozens of times (e.g., three to four times in *Dalechampia*; Armbruster 1993; and several times in Catasetine orchids; Chase and Hills, 1992), indicating frequent specialization on new pollinators. The specialized reward system based on secretion of floral resins involves only a few genera of bees that build their nests out of resin. Although the reward system has evolved only three or four times in the angiosperms, the relationship is employed by several hundred species of plants occurring in most lowland tropical habitats worldwide (Armbruster, 1984). Finally, the relationship between figs and their seed-feeding wasp pollinators is extremely specialized, and involves some 900 plant species, also occurring worldwide in nearly all lowland tropical forest habitats (see Wiebes, 1979; Janzen, 1979; Herre and West, 1997).

Ollerton (1998; this volume) has pointed out that the predictive power of syndromes have never been tested. Indeed the most narrow and highly derived definitions of syndromes as presented by Faegri and van der Pijl (1966; 1971; 1979) have never been fully evaluated or tested. It is clear that not all syndrome components (traits) are robustly predictive; e.g., blossom color is a notoriously poor predictor of pollinator; Armbruster, 1996a; Waser et al., 1996; Waser and Price, 1998). Thus narrowly defined syndromes also lack robust predictive power (see Ollerton, 1998; Waser and Price, 1998). But if we instead define syndromes on the basis of reward chemistry, the predictive power of reward

syndromes is so high as hardly to need statistical testing. Most oil-secreting flowers are pollinated primarily by oil-collecting bees, fragrance-reward flowers by male euglossine bees, resin-reward flowers by resin-collecting bees, pollen-reward flowers by pollen-feeding animals, and nectar-reward flowers by nectar feeding animals (Armbruster, unpubl. observations).

Indeed it seems more instructive to think about using reward chemistry, fragrance chemistry, flower color, and other floral traits to explain portions of the among-species variance in pollinators (and vice versa: using pollinators to explain the variation in different floral traits). We argue that most of the explainable variance will be related to reward type. Whether significantly additional variance is explained by fragrance chemistry, flower color, or corolla shape remains to be evaluated (but see Ollerton, this volume). We expect these other components explain much smaller, but still significant, portions of the total varaince.

Our point is that pollination ecology is better interpreted as ecological variance that can be partitioned into various components explained by floral, animal, and environmental factors, rather than interpreted as a fixed ecology predicted (or not) by a particular floral syndrome. 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 ecological interactions in contemporary time. That such dynamic complexity ever converges on the traditional, multi-trait pollination syndromes (see Ollerton, this volume) is what is remarkable, not that it does so incompletely.

Ollerton (1996) raised the point that the present suite of convergent traits that we observe for a given hypothetical pollination syndrome reflects past selection. It is possible that some sort of evolutionary inertia (e.g., genetic or developmental constraints or homeostasis) may prevent response to selection for traits that we associate with generalized pollination syndromes. This may help explain Ollerton's paradox, why

evolutionary specialization seems to be important and common, yet we observe lots of ecological generalization, i.e., pollination by many different animal species. Once evolved, the complexity of biosynthesis and the associated relationship may restrict evolutionary change, even in the face of fluctuating and disruptive selection by multiple pollinators (Stebbins, 1974). For example, *Lavandula* is pollinated by dozens of different pollinators, some of which vary from the predicted bee pollination mode (Herrera, 1988) without any evidence of adaptation response. *Dalechampia bernieri* is pollinated by tiny *Liotrigona* bees near Morondava, Madagascar (Armbruster et al., 1994), but still retains adaptations for buzz pollination by huge carpenter bees as occurs in the north of the island.

This inertia may reflect lack of sufficient genetic variation (Bradshaw, 1991). Indeed, as Stebbins (1970; 1974) suggested, pollination syndromes are clusters of covarying, "coadapted" traits, which perhaps evolve during periods of rapid divergence in response to selection by principal pollinators. These trait clusters may be maintained today by genetic/developmental constraint or even homeostasis, despite directional or disruptive selection by varied pollinators. Genetic variation off the correlation trajectory may be very limited. Thus, a period of evolution in response to selection generated by a single class of pollinators may lead to rapid evolution of integrated, homeostatic trait clusters (syndromes), followed by stasis in face of disruptive/directional selection by diverse pollinators (see Stebbins, 1974; Ollerton, 1996). As a specialized syndrome evolves, a number of morphological traits are fixed and not easily changed by fluctuations in abundance and importance of pollinators and selective pressures. Developmental canalization may be due to the evolution of strong genetic buffering of the trait, or mutations leading to the disruption of the trait may have such drastic pleiotropic consequences that they rarely have the opportunity to spread. Perhaps this may explain the patterns documented by Ollerton (this

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1e to the evolution of
ring of the trait, or
the disruption of the
rastic pleiotropic con-
arely have the oppor-
1aps this may explain
1ted by Ollerton (this

volume) whereby certain pollination syndromes appear to cluster together in phenotypic space.

Alternatively, as Ollerton (this volume) recognizes and as we have discussed above, the lability of pollination systems argues against any internal constraints, suggesting instead, the importance of stabilizing selection in maintaining any observed stasis. Indeed, the observation that mutations can alter symmetry patterns in flowering plants (e.g., Cubas et al., 1999), that selection can lead to changes in taxonomically conservative traits (Heuther, 1968), and that destabilized phenotypes can be recanalized at different states (Rendel, 1967) all argue strongly for a pervasive role of stabilizing selection and its developmental analog (canalizing selection) for the maintenance of suites of traits associated with pollination syndromes (reviewed in Fenster and Galloway, 1997).

It is difficult to choose among these hypotheses. We lack sufficient information about the genetic basis of floral integration to evaluate the developmental constraint hypothesis. Studies investigating the genetic basis of multi-trait syndrome are clearly needed. Artificial selection and quantification of the pleiotropic consequences of mutations are two such methods. Comparative approaches, through mapping multiple character-state changes along sufficiently resolved phylogenies, may also contribute to our understanding of the origins and maintenance of trait integration.

CONCLUSIONS

We think that the diversity of opinions noted in this essay (even amongst ourselves) reflects the dynamics and health of modern pollination ecology. To paraphrase Knut Fægri's comments (pers. comm.) at the most recent meeting of the Scandinavian Pollination Ecologists meeting (SCAPE), differences of opinion among biologists are healthy and stimulating, and reflect activity in the field. Indeed, pollination biology is today more vigorous and vibrant than ever, in part, we think, because it

sits at the nexus of three dynamic fields: evolution, ecology, and behavior.

We suspect, however, that some present disagreements in pollination ecology may be based on misunderstanding instead of true difference of opinion. For example, it seems important to keep clear in our minds the difference between the evolutionary process of specialization and the ecological state of being specialized. We suggest that in the context of plant-pollinator evolution, studies of evolutionary specialization are just as important as studies of the current ecological state of specialization. We also need to think carefully about the relationship between specialization on species of pollinators versus on functional groups of pollinators. We argue that specialized adaptations and syndromes are usually generated and maintained by selection created by classes of similar pollinators, and only rarely by single pollinator species. This should not cause us to reject the importance of specialization. By analogy, consider that we have not rejected the widespread importance of coevolution in the evolution of plant-animal relationships just because there are few examples of 1:1 coevolution.

We need to think more carefully and critically about pollination syndromes. Despite our deep skepticism about syndromes as tight phenotypic/ecological units, we feel that the concept has much to offer as an initial model of flower evolution. We should avoid defining pollination syndromes so narrowly that they lose all value. We need to come to agreement about how much predictive power pollination syndromes must have to be useful. Are syndromes useful if they explain only a portion of the variance in pollinator type? We think so. Are they useful if reward chemistry explains considerable variance, but the color component much less? Probably so. We should not be surprised to find that the number of exceptions to a syndrome nearly equals the number of observations conforming to the expected trend. Finally, we think one of the most exciting areas of research on pollination syndromes will come from investigating the relative contribution of contemporary selection by pollinators

versus genetic and developmental constraints or homeostasis to the maintenance of each syndrome.

To these ends, we have proposed a number of approaches to quantify the origin, maintenance, and evolution of specialized and unspecialized pollination ecology, as well as the combinations of floral traits that have been recognized as pollination syndromes. We hope that these experimental and comparative approaches will be used more widely in the future and lead to a better understanding of the role of specialization in the evolution of flower-pollinator relationships.

Having interacted with Knut Fægri at SCAPE meetings over the past few years, we conclude that he certainly never intended to write the final chapter on pollination biology, but rather hoped to encourage new ideas and approaches. The framework that Fægri and van der Pijl constructed in *Principles of Pollination Ecology* for studying and testing pollination systems has been clearly successful.

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