

Competition Drives Specialization in Pollination Systems through Costs to Male Fitness

Nathan Muchhala,^{1,*} Zachary Brown,² W. Scott Armbruster,³ and Matthew D. Potts⁴

1. Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario M5S 3G5, Canada; 2. Department of Computer Science, University of Miami, Coral Gables, Florida 33124; 3. School of Biological Sciences, University of Portsmouth, Portsmouth PO1 2DY, United Kingdom; Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775; and Department of Biology, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway; 4. Department of Environmental Science, Policy, and Management, University of California, Berkeley, California 94720

Submitted April 21, 2010; Accepted August 24, 2010; Electronically published October 18, 2010

Online enhancement: zip file.

ABSTRACT: Specialization in pollination systems played a central role in angiosperm diversification, yet the evolution of specialization remains poorly understood. Competition through interspecific pollen transfer may select for specialization through costs to male fitness (pollen lost to heterospecific flowers) or female fitness (heterospecific pollen deposited on stigmas). Previous theoretical treatments of pollination focused solely on seed set, thus overlooking male fitness. Here we use individual-based models that explicitly track pollen fates to explore how competition affects the evolution of specialization. Results show that plants specialize on different pollinators when visit rates are high enough to remove most pollen from anthers; this increases male fitness by minimizing pollen loss to foreign flowers. At low visitation, plants generalize, which minimizes pollen left undispersed in anthers. A model variant in which plants can also evolve differences in sex allocation (pollen/ovule production) produces similar patterns of specialization. At low visitation, plants generalize and allocate more to female function. At high visitation, plants specialize and allocate equally to both sexes (in line with sex-allocation theory). This study demonstrates that floral specialization can be driven by selection through male function alone and more generally highlights the importance of community context in the ecology and evolution of pollination systems.

Keywords: generalization, community context, competition through heterospecific pollen transfer, simulation model.

It is widely accepted that evolutionary specialization has played a major role in the diversification of life (Futuyma and Moreno 1988). A good example of this is found in flowering plants, where specialization in pollination systems has been invoked as a central process driving divergence and diversification (Grant 1949; Stebbins 1970). In support of this idea, phylogenetic evidence shows that an-

giosperm taxa with derived floral traits associated with increased specificity (e.g., nectar spurs, zygomorphy) tend to be more species rich than their sister taxa (Hodges and Arnold 1995; Sargent 2004; Ree 2005; Kay et al. 2006; Kay and Sargent 2009) and that increased pollinator specialization correlates with increased species richness among orchid clades (Schiestl and Schluter 2009). However, we still lack a solid understanding of the factors that favor specialization in pollination systems (Fenster et al. 2004).

Populations do not occur in isolation, and community context can heavily influence evolution along the specialization-generalization continuum. In particular, strong interactions with competitors can select for increased specialization (Schluter 2000). For plants, sharing pollinators can lead to competition through either loss of visits or interspecific pollen transfer (Rathcke 1983; Waser 1983). Although competition has been recognized as a force promoting specialization on different pollinators (e.g., Waser 1983; Armbruster and Herzig 1984), this idea is neglected in many reviews of specialization and pollination syndromes (Waser et al. 1996; Johnson and Steiner 2000; Fenster et al. 2004; Gomez and Zamora 2006; but see Armbruster 2006). Furthermore, theoretical models of pollinator specialization typically treat plant species in isolation, thus overlooking the community context (Kiestler et al. 1984; Waser et al. 1996; Wilson and Thomson 1996; Aigner 2001). An exception is the population genetic model developed by Sargent and Otto (2006), which demonstrated that abundance among competitors is critical, in that rare species tend to evolve specialization.

When considering the negative effects of interspecific pollen transfer, it is important to distinguish between male and female components of plant fitness. While recognized as theoretically important (e.g., Charnov 1979; Bell 1985; Morgan 1992; Schoen and Ashman 1995), the male component of fitness has been evaluated empirically far too

* Corresponding author; e-mail: n_muchhala@yahoo.com.

infrequently (but see Stanton et al. 1991; Conner 1997; Irwin and Brody 2000; Strauss et al. 2001; Lau et al. 2008). Interspecific pollinator movements decrease male fitness because the probability that pollen will be dispersed to suitable mates is reduced when pollen is lost during visits to foreign flowers. Although very few empirical studies have demonstrated this cost (but see Campbell 1985; Campbell and Motten 1985; Flanagan et al. 2009), the negative impact seems clear when one considers that plants produce a finite quantity of pollen and selection will favor maximizing the number of grains that reach conspecific stigmas (Aigner 2001; Thomson 2003; Harder and Routley 2006). For the female component, the deposition of foreign grains on a stigma can decrease fitness by blocking the stigmatic surface, clogging the style with foreign pollen tubes, or producing inviable seeds or low-fitness hybrid offspring. Empirical work has shown a range of outcomes (reviewed in Morales and Traveset 2008), from no detectable effect (Kwak and Jennersten 1991; Murcia and Feinsinger 1996) to strong fitness reduction (Thomson et al. 1981; Armbruster and Herzig 1984; Waser and Fugate 1986; Caruso and Alfaro 2000). Thus, while costs to the male component are relatively clear, costs to the female component are less clear and are likely to be highly system specific.

The male component of fitness is not fully addressed in the few previous theoretical treatments of competition for pollination. For example, Levin and Anderson (1970) define fitness as the percent of a flower's ovules that are successfully fertilized, ignoring the number of pollen grains the flower disperses. Montgomery (2009) similarly defines a plant's reproductive success solely in terms of pollen receipt. Sargent and Otto (2006) track pollen transfer from male to female flowers; however, they implicitly assume that flowers have unlimited amounts of pollen. In their model, male fitness of a given flower is limited only by the number of visits it receives (also see Kiester et al. 1984 for a similar assumption); thus, any negative impacts of interspecific pollen transfer on male function do not manifest. In fact, these conditions always favor generalization and the ability to attract as many pollinators as possible; to enable the evolution of specialization, they assume fitness trade-offs in adapting to more than one pollinator. Rodríguez-Gironés and coauthors (Rodríguez-Gironés and Santamaría 2007; Rodríguez-Gironés and Llandres 2008) do incorporate costs to male fitness in their models of the evolution of orchid spur length, since each flower produces two pollinia. However, their models also include costs to female fitness (foreign pollen grains fertilize ovules and produce inviable seeds); thus, it is difficult to separate the degree to which the male versus female costs select for specialization. Additionally, when each plant possesses 10 pollen grains rather than two pollinia,

specialization fails to evolve (Rodríguez-Gironés and Llandres 2008). It is unclear why pollen quantity affects specialization and whether results are generalizable beyond orchids, given that most flowers produce many loose grains of pollen.

In this article, we develop individual-based models with two plant species and two pollinator types to study the effects of competition on the evolution of specialization in pollination systems. Our goal is to isolate the male fitness cost (pollen loss) to determine whether this alone can drive specialization. To this end, we do not include trade-offs in adapting to more than one pollinator. For pollination systems, an adaptive trade-off could be imposed by the nature of flower and pollinator traits; for example, wide corollas fit bat snouts better, while narrow corollas are better for hummingbird bills (Muchhala 2007). Alternatively, trade-offs could be due to limited resources available to a flower; for example, limited sugar production could preclude secreting nectar during the day and night (to attract diurnal and nocturnal visitors). Clearly, the more trade-offs that exist and the stronger they are, the more likely it is that specialization will evolve (Wilson and Thomson 1996; Aigner 2001; Kay and Sargent 2009), but can it evolve in their absence?

For specialization to occur in the absence of trade-offs, flowers must evolve filter traits (sensu Johnson et al. 2006) that exclude a subset of the potential floral visitors in their habitat. For example, flowers of *Gesneria quisqueyana* remain open for several nights yet close during the day to exclude diurnal visitors (Martén-Rodríguez et al. 2009). However, flower characteristics cannot always control visitor identity this precisely. Pollinators can learn and will readily switch to exploit unused resources. For example, hummingbirds visit bat-pollinated *Burmeistera* even though their flowers have evolved an inconspicuous green color (Muchhala 2003). Although complete specialization on different pollinators may not always be possible, selection should still favor partial filter traits that minimize visitation by certain pollinators.

For our initial analyses, we further isolate male fitness costs by assuming no cost to the deposition of foreign pollen on stigmas (the female component), fixing each plant population at equal abundances, and assuming each pollinator is equal in terms of effectiveness. To better understand selection on male function, we track pollen fates (sensu Johnson et al. 2005; Harder and Routley 2006) for each flower, noting the number of grains successfully dispersed to conspecific stigmas, lost during the various stages of transport, or left undispersed in the anthers. In later model variants, we explore the effects of (1) allowing pollen : ovule ratios to evolve, (2) adding a cost to receiving foreign pollen, (3) allowing only partial filter traits to

evolve, and (4) eliminating the transfer of foreign pollen to stigmas.

The Model

Here we describe the basic version of the model with a number of starting parameters (summarized in table 1). We systematically varied these parameters in later analyses. Two plant species (A and B) and two pollinator types (X and Y) interact in the model. Each plant is diploid, with one set of genes that controls attraction of pollinator X and another set for pollinator Y. Each set has five loci, and each locus is diallelic (0 or 1), with additive effects on the phenotype such that the total attraction value of that plant for that pollinator varies from 0 to 10. This corresponds to the probability that the pollinator will visit the flower (from 0% to 100%) when encountered. Since we are primarily interested in addressing evolutionary rather than ecological questions, plant population sizes were not allowed to fluctuate or to be driven to extinction but rather were fixed at 50 individuals for each species. Each plant individual has one perfect flower (i.e., with male and female parts) that produces 500 pollen grains and five ovules. Each gamete (pollen or ovule) is haploid, with the allele for each locus selected at random from the two corresponding parental alleles. Loci are unlinked (i.e., assort independently).

For each simulation, the evolution of plant species A and B was followed through 1,000 generations to determine whether each population specializes on one pollinator or generalizes on both. In each generation, 40 individuals of each pollinator type (X and Y) moved through the community in a random order until each made 40 flower visit attempts. For each visit attempt, a pollinator was drawn at random (from among those that had not yet completed 40 visit attempts), a plant was drawn at random (from the pool of 100; 50 of A and 50 of B), and the attraction of the plant for that pollinator type (0%–100%) was compared to a randomly generated number (0–100; uniform distribution). If the random number was greater, the pollinator visited the plant's flower. Regardless of whether a visit was made, a counter tracking the number of visit attempts by this individual was then decreased by 1. This process continued until all 80 pollinators (40 of X and 40 of Y) made 40 visit attempts. Each time a pollinator visited a flower, it deposited up to five pollen grains from its body onto the stigma and then picked up 50 pollen grains from the anthers. After each visit, 20% of the pollen on the pollinator was lost at random (due to grooming or falling off during flight). After all pollinator individuals completed all visits, the five ovules of each flower were fertilized by conspecific pollen selected at random from that present on the stigma. In the basic model, heteros-

Table 1: Parameters used in the model and parameter values for the basic version of the model

Parameter	Value in basic model
Plants:	
No. plant species	2 (A and B)
No. plant individuals	50
No. flowers per plant	1
No. pollen grains per flower	500
No. ovules per flower	5
Pollinators:	
No. pollinator types	2 (X and Y)
No. pollinator individuals	40
No. visits by each individual	40
No. pollen grains picked up	50
No. pollen grains deposited	5
Pollen loss rate (%)	20

pecific pollen on the stigma was ignored. The diploid genotype of each fertilized seed was assigned by combining the haploid genotypes of the gametes. Of all the fertilized seeds produced by each plant species (A or B), 50 were selected at random to grow into plants to represent the following generation.

Before the first generation of each model run, the alleles for each plant were randomly assigned following a uniform distribution. At the end of the 1,000 generations, we analyzed the genetic composition of each plant population to examine the extent to which specialization or generalization evolved. The model was implemented in Sun Java. Model documentation, an executable model, and documented source code may be downloaded from <http://code.google.com/p/modelframe/downloads/list> or is available in a zip file in the online edition of the *American Naturalist*.

Results

Basic Model

In the basic model (see table 1), which has 1,600 visits per generation (40 pollinator individuals of each type making 40 visits), by the thousandth generation, specialization on different pollinators always evolved (fig. 1). Which plant (A or B) specialized on which pollinator (X or Y) varied between runs, as expected given that parameters were identical for the two pollinators. As visits per generation were increased above 1,600 in additional runs of the model, the greater the visit rate was, the faster the plants specialized. When visits were decreased below approximately 900 visits per generation (through either fewer pollinator individuals or fewer visits per pollinator), both plants became generalists (fig. 2A). To better understand the mechanisms that drive these results, we tracked pollen fates for these

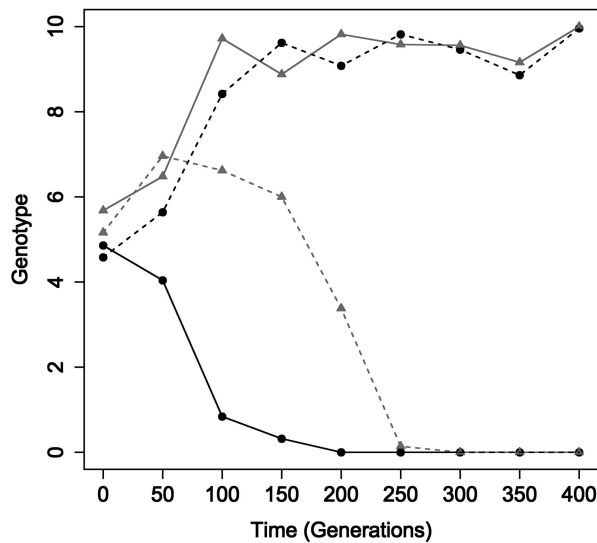


Figure 1: Evolution of pollinator attraction genes of plant A (triangles) and plant B (circles) for pollinator X (solid lines) and pollinator Y (dashed lines) over the first 400 generations in a sample run of the basic model (see table 1 for parameters). Note that each plant specializes on a different pollinator; specialization always evolved in 100 repeat runs.

runs. Every 50 generations, we determined the mean proportion of the 500 grains each plant produced that (a) remained in the anthers (e.g., removal failure; Harder and Routley 2006), (b) were removed but remained on pollinators' bodies at the end of the generation, (c) were removed but were shed/groomed during subsequent visits to heterospecifics, (d) were removed but were shed/groomed during subsequent visits to conspecifics, (e) were dispersed to heterospecific stigmas, or (f) were dispersed to conspecific stigmas (see fig. 3). Only fate *f* can contribute to male fitness; thus, any evolutionary changes that increase *f* by decreasing *a–e* will be selected for. Specialization increases fitness by decreasing the amount of pollen lost during visits to heterospecific flowers (fate *c*) or dispersed to heterospecific stigmas (fate *e*). However, when visit rates were especially low, plants evolved generalization because the number of grains left in the anthers (fate *a*) was high; pollen removal in this case is maximized by attracting both types of pollinators (fig. 3A). When visit rates were high enough to remove the majority of pollen, the two species specialized on different pollinators because this decreases pollen loss during visits to heterospecific flowers (fig. 3B).

We systematically varied other parameters to fully explore the model. Varying pollen deposition per visit or pollen loss rate had no effect on results shown in figure 2A. Moderate changes in ovule number per plant similarly did not affect results (but see below). Increasing pollen

production per flower increased the number of visits needed to favor specialization, since more visits are needed to remove all pollen. Decreasing pollen pickup per visit also increased the point at which specialization is favored, again because more visits are needed to remove all pollen. Finally, we increased plant population sizes up to 1,000 individuals to determine the potential impact of genetic drift in small population sizes. There were no qualitative differences in results between these runs and those with 100 individuals. Overall, results suggest that the critical determinant of whether specialization is favored involves whether plants are receiving enough visits to remove their pollen. Increasing visits or pollen pickup per visit favors specialization, while increasing pollen per flower or decreasing visits favors generalization.

Large increases in ovule number per flower reduced the tendency to specialize. Figure 4 shows this effect for the basic model as the ovule number per flower is increased. Very high ovule numbers (>60) create a pollen-limited environment (Knight et al. 2005), where there are more ovules per plant than the number of pollen grains the plant receives. This introduces selection via female fitness to generalize in order to receive more visits and increase seed set. At very high ovule numbers, this selection often overpowered selection via male fitness to specialize, although about 20% of runs still evolved specialization (fig. 4).

We also varied the nature of pollen deposition. Instead of depositing a constant number of grains, pollinators deposited a percent of the grains they were carrying. This caused a slight decrease in the evolution of specialization; for example, even at the highest visit rates, specialization occurred in only 96% of the runs. However, the overall pattern did not change; as in figure 2A, generalization was favored with fewer than approximately 900 visits per generation (see fig. A1, available in a zip file in the online edition of the *American Naturalist*). In the same way that varying the absolute deposition amount did not affect results, varying proportional deposition from 5% to 20% did not affect this pattern.

Variant 1: Evolution of Pollen : Ovule Ratios

In the basic model, whether specialization evolves depends on the number of visits received relative to the amount of pollen produced. At higher visit rates or less pollen per flower, plants respond to the costs of interspecific pollen transfer by specializing. However, what would happen if plants also had the option of evolving greater amounts of pollen production in the face of higher visit rates? Would this affect the evolution of specialization? For this model variant, we allow plants to evolve differences in pollen production by giving each plant a set quantity of resources

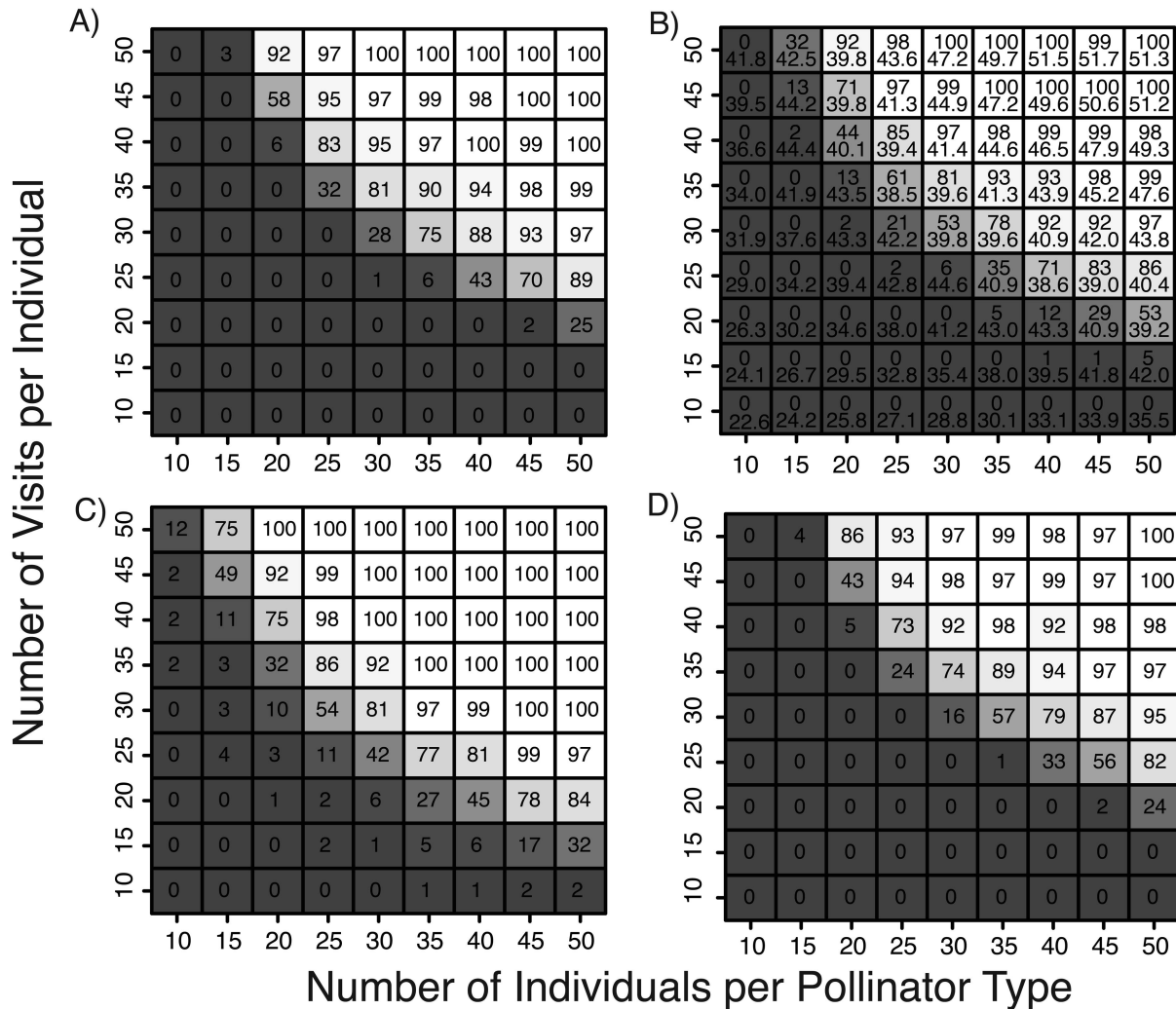


Figure 2: Summary of model results given different visit rates, in terms of the number of pollinator individuals of each type and the number of visits each makes per generation. Each cell shows the number of repeat runs, out of 100, in which the two plant species specialized on different pollinators (*white*, >90% specialization; *dark gray*, >90% generalization). A, Results for the basic model. B, Results for variant 1, which adds the evolution of pollen : ovule ratio; the lower number in each cell is the mean percent investment in male function. C, Results for variant 2, which includes costs to female function; foreign pollen that arrives on stigmas fertilizes ovules, resulting in inviable seeds. D, Results for variant 3, which allows evolution of only partial filter traits; attraction for different pollinators can evolve only between 20% and 100% (vs. between 0% and 100% in the basic model).

that can be allocated to either male function (number of pollen grains) or female function (number of ovules). The pollen : ovule (P : O) ratio is controlled by a third set of genes consisting of 50 loci that each have two alleles (0 or 1). The sum of these numbers (range 0–100) corresponds to the proportion of resources that the plant invests in male function (0%–100%). For initial analyses, plants were given 1,000 resource units, and the cost of one ovule was set to 100 pollen grains, such that a plant that invests 50% in male function produces 500 pollen grains and five ovules. Alleles for each plant, for both attraction and

P : O genes, were drawn randomly from a uniform distribution before the first generation of each model run.

Overall, results of the basic model were not changed by this variant (fig. 2B; cf. fig. 2A): generalization was favored when visit rates were less than approximately 900 per generation, and specialization was favored at higher visit rates. In this variant, as the number of visits decreased, the proportion that plants invested in male relative to female function also decreased. This is because with lower visits, increasing numbers of pollen grains are left in anthers (i.e., pollen fate *a*), which introduces a saturating gain curve

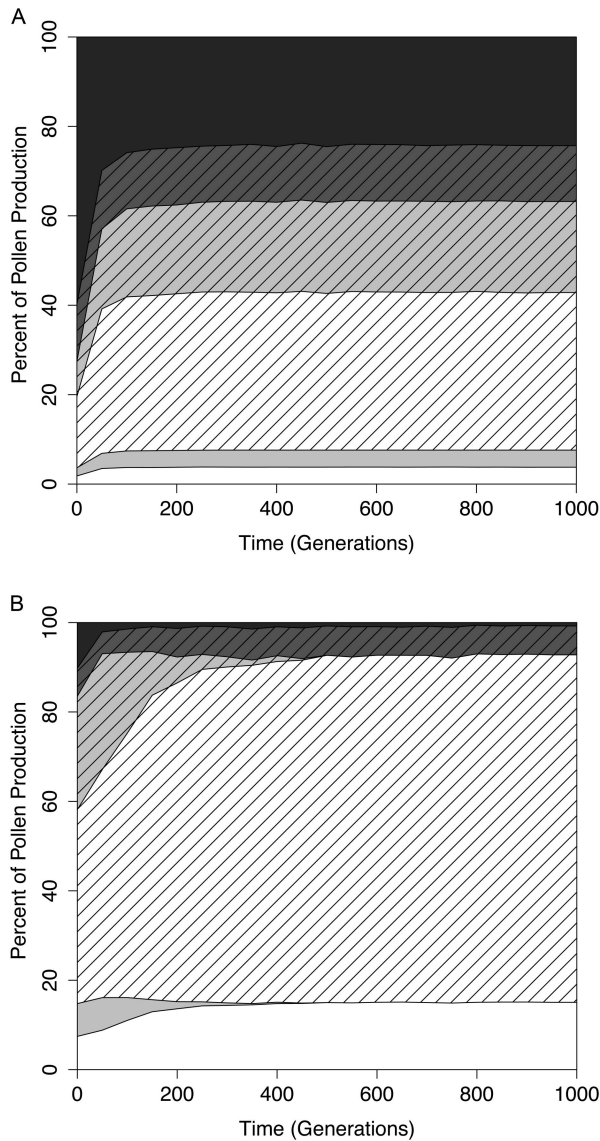


Figure 3: Pollen fates when (A) generalization evolves at low visit rates (20 individuals and 20 visits per generation) and (B) specialization evolves at high visit rates (40 individuals and 40 visits per generation). Shown are 100 model runs, listed from top to bottom, for the mean proportion of a plant's pollen production that (a) fails to be removed from the anthers (*dark gray*), (b) is removed but remains on the pollinator's body (*hatched gray*), (c) is removed but shed/groomed during visits to heterospecifics (*hatched light gray*), (d) is removed but shed/groomed during visits to conspecifics (*hatched white*), (e) is dispersed to heterospecific stigmas (*light gray*), or (f) is dispersed to conspecific stigmas (*white*).

for male fitness. Put simply, it does not help to produce more pollen per flower if it is not removed from the anthers. Male gain curves can be visualized as the male investment (in terms of number of grains produced) plotted against male fitness (in terms of number of grains suc-

cessfully dispersed to conspecifics). In figure 5 we show male gain curves for all 100 plants in the first generation of the model (which start with randomly assigned male investment values, 0%–100%) at low visitation (fig. 5A) versus high visitation (fig. 5B). Note that the gain curve rapidly saturates at low visits. The female gain curve, on the other hand, is always linear in our model. In line with predictions of sex allocation theory (Charnov 1979; Charlesworth and Charlesworth 1981; Lloyd 1984; Brunet 1992), the faster the male gain curve saturates, the lower the optimal investment is in male function. When visits are increased, the male gain curve becomes more linear and investment in male function increases until plants invest approximately equally in male and female function. Again, as predicted by sex allocation theory (Maynard Smith 1971; Charnov 1982; Lloyd 1984), when male and female gain curves have a similar shape, the optimal strategy is equal investment in male and female function. When visits are further increased, plants continue to evolve 50% male investment, but specialization begins to be favored since this decreases pollen loss to foreign flowers.

Decreasing the relative cost of ovules versus pollen decreases the tendency to specialize. Cheaper ovules mean more are produced relative to pollen grains. Thus, this change has an effect similar to increasing ovule production in the basic model (e.g., fig. 4): it creates a pollen-limited environment that introduces selection on female function

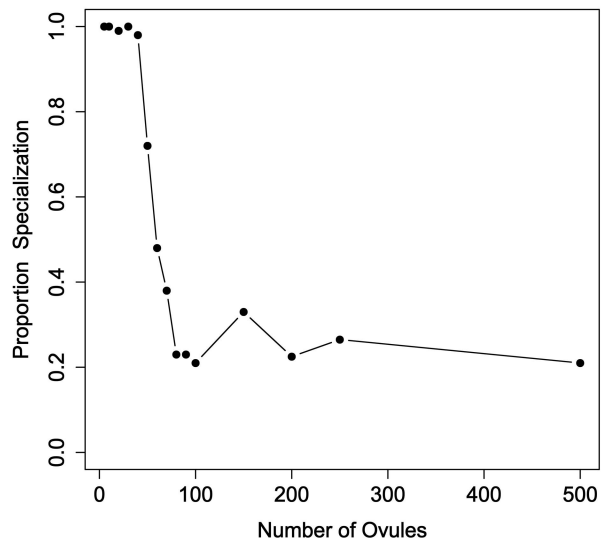


Figure 4: Effects of varying ovule number on specialization in the basic model (see table 1 for other parameters). Dots represent the proportion of model runs (out of 100) in which both plants evolve specialization on different pollinators as the ovule number per plant is varied from five to 500.

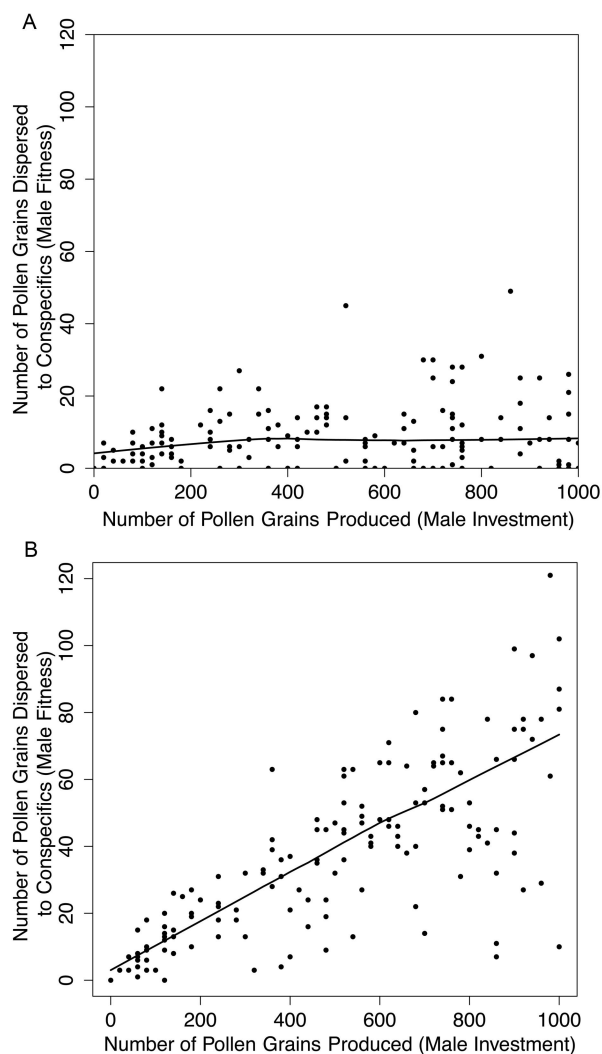


Figure 5: Fitness gain curves for male function at (A) low visit rates (20 individuals and 20 visits per generation) and (B) high visit rates (30 individuals and 30 visits per generation). The figure shows the relationship between how many grains of pollen individual plants produce in the first generation of the model and the number of these grains successfully dispersed to conspecifics (i.e., fitness). At low visit rates, higher pollen production leads to diminishing returns in terms of fitness because of the large numbers of pollen grains that remain in the flower undispersed; this selects for low pollen : ovule ratios. At high visit rates, male fitness gain curves are linear, which selects for equal investment in male and female function. LOWESS curves were fitted in each panel to make the relationship easier to visualize.

to generalize in order to receive more visits and increase seed set.

Variant 2: A Cost to Receiving Foreign Pollen

The basic model assumes that no fitness costs are incurred when a stigma receives foreign pollen; only conspecific

pollen fertilizes ovules, and the number of foreign pollen grains present is irrelevant. In this variant, foreign pollen decreases female fitness by fertilizing ovules and creating inviable seeds. The pollen selected to fertilize each ovule was chosen at random from all pollen present (conspecific and foreign) rather than from just the conspecific pollen. The addition of female costs causes specialization to evolve at lower visit rates than observed in the basic model (fig. 2C).

Variant 3: Partial Filter Traits

In the basic model, we assume that strong filter traits can evolve to exclude pollinators completely (e.g., an attraction of 0% for that pollinator). However, as noted in the introduction, floral traits typically cannot control visitation patterns this precisely. Here we examine whether specialization is still favored when plants can evolve only partial filter traits. In this variant, plants can reduce visit rates only to 20% (rather than 0%). Attraction genes are the same as in the basic model, but when a plant possesses attraction genes that sum to less than 2, the attraction is set to 20%. Results show an overall pattern similar to that of the basic model; even though plants cannot evolve complete specialization, at high visit rates each plant maximizes attraction of one pollinator and minimizes attraction of the other (fig. 2D).

Variant 4: No Foreign Pollen Transfer

For this variant, pollinators did not transfer foreign pollen. Stigmas received only conspecific pollen and thus did not affect the amount of foreign pollen present on the pollinator. In nature, this can occur if competing plant species place their pollen on different parts of pollinators' bodies (e.g., Armbruster et al. 1994; Muchhala and Potts 2007). Results show a moderate increase in the number of visits needed to favor specialization (from ~900 to ~1,200; see fig. A2, available in a zip file in the online edition of the *American Naturalist*). Thus, while diverging in pollen placement reduces the costs to male fitness that favor specialization, it does not completely eliminate them.

Discussion

In our model, competition through interspecific pollen transfer selects for specialization on different pollinators when visit rates are high enough to remove most of the pollen from the anthers (fig. 1). Specialization serves to minimize pollen loss during visits to foreign flowers and thus maximize pollen successfully transferred to conspecifics (fig. 3B). When visit rates are low, generalization on multiple pollinator types is favored because this minimizes

the amount of pollen left undispersed in anthers (fig. 3A). Allowing plants to evolve changes in P : O ratios does not alter these qualitative results; generalization evolves at low visit rates and specialization at high visit rates (fig. 2B). In line with sex allocation theory (Charnov 1979; Charlesworth and Charlesworth 1981; Lloyd 1984), when visit rates are low enough to impose diminishing returns on male fitness allocation (see fig. 5), the plants evolve to allocate less to pollen production relative to ovule production. When visit rates are high enough to adequately remove pollen, plants evolve to split resources evenly between male and female function (e.g., pollen and ovule production), and specialization is favored (fig. 2B).

An important conclusion of our model is that selection through male function alone can lead to specialization. As noted in the introduction to this article, male function is usually overlooked in studies of plant fitness; our results underscore its potential importance for floral evolution. The few previous models of competition for pollinators focus on female function (Levin and Anderson 1970; Sargent and Otto 2006; Montgomery 2009). Rodríguez-Gironés and coauthors (Rodríguez-Gironés and Santamaría 2007; Rodríguez-Gironés and Llandres 2008) do model both male and female function in their analyses of orchid spur length evolution, but they incorporate costs to both genders, and character displacement in the moth pollinators causes different moths to visit different plants, so it is unclear which of these factors selects for specialization. In our model, there are no costs to female function (style clogging/stigma blockage), although variant 2 demonstrates that the addition of such costs amplifies the tendency to specialize (fig. 2C). Our model also lacks trade-offs in adapting to different pollinators. Trade-offs may be widespread in pollination systems (Aigner 2001; Sargent and Otto 2006; Muchhala 2007), and adding them would clearly increase the tendency to specialize, but they are not necessary for specialization to occur. Furthermore, the two pollinators in our model were identical in terms of visit rates and effectiveness. Thomson (2003) suggested that differences in effectiveness can select for specialization because a poor pollinator can be thought of as a conditional parasite; it will be a mutualist if it is the only pollinator available but becomes a parasite in the presence of a better pollinator because it wastes pollen that could have been more efficiently dispersed. Thus, even in the absence of female costs, pollination trade-offs, or pollinator differences, costs to male function alone can select for specialization.

In order to specialize, the plants evolve to exclude one of the pollinator types. Even in instances where they cannot be completely excluded, plants still evolve partial filter traits that reduce visit rates of the unwanted pollinator (fig. 2D). Recent evidence suggests that examples of filter

traits may be widespread among angiosperms (e.g., Castellanos et al. 2004; Johnson et al. 2006; Kessler et al. 2008; Forrest and Thomson 2009; Shuttleworth and Johnson 2009), and other theoretical work also stresses their importance (Rodríguez-Gironés and Santamaría 2005). Thus, our study joins mounting evidence supporting the idea that pollination syndromes should be thought of as a collection of traits that evolved not only in response to the primary pollinator but also to discourage visits by other potential pollinators (Pijl 1961).

Analyses of pollen fates in the model (fig. 3) highlight the importance of receiving enough visits to remove most of the pollen from anthers. Either decreasing visit rates or increasing pollen production favors generalization. We suggest that this clarifies an initially puzzling result in the model by Rodríguez-Gironés and Llandres (2008). They found that specialization failed to evolve when the orchids possessed 10 (rather than two) pollinia and similarly failed to evolve when flower life span was reduced to one-tenth the baseline value, a change that caused the mean number of visits received per flower to decrease from 20 to two. Our analyses suggest that selection on the plants under these circumstances favors generalizing because generalists receive enough visits to remove pollen from the anthers.

To what extent do angiosperms receive enough visits to remove their pollen in nature? In a review of monocot pollination systems, Harder (2000) found that orchid pollinia are removed from flowers only around half of the time, while species with granular pollen (the typical angiosperm condition) have quite low removal failure rates (median 6.6%). A handful of other studies all found pollen removal rates (typically per hour or per day) that were more than sufficient to remove all of the flower's pollen through its life span (Johnson et al. 1995; Rush et al. 1995; Vaughton and Ramsey 1998; Kudo and Harder 2005). These data suggest that male fitness is not typically limited by insufficient pollen removal and therefore that selection to reduce pollen loss during visits to foreign flowers may be fairly common. Note that our model allows plants to respond to this selection only by specializing on different pollinators; other possible evolutionary responses include flowering at different times of the day or year (Stone et al. 1998) or placing pollen on different regions of pollinators' bodies (Armbruster et al. 1994; Muchhala and Potts 2007).

Analyses of pollen fates also allow us to compare the relative importance of different forms of pollen loss. Interestingly, of the pollen lost during visits to foreign flowers, only ~20% is lost to foreign stigmas; the majority is groomed/shed by the pollinator (fig. 3a, cf. *gray*, *hatched gray*). This is in accord with the two empirical studies we are aware of that track pollen fates in sufficient detail; Murcia and Feinsinger (1996) and Flanagan et al. (2009)

found that pollinators lost large amounts of pollen during visits to foreign flowers but only a small fraction of this was actually deposited on the foreign stigmas. Most reviews of competition for pollination mention only pollen loss to foreign stigmas (Rathcke 1983; Waser 1983; Morales and Traveset 2008; but see Mitchell et al. 2009). One important implication of these results is that diverging in pollen placement will not completely eliminate the negative effects of interspecific pollen transfer for male fitness (although it will for female fitness). This can be seen in variant 4: eliminating foreign pollen transfer to stigmas decreases the tendency to specialize somewhat, but specialization still occurs when visits are high enough.

The selection through male function to diverge from competitors may be nearly ubiquitous among angiosperms. As long as a plant species shares pollinators with other species, it could lose pollen during visits to foreign flowers. This competitive mechanism can be easily overlooked because pollinators need not be a limiting resource (unlike other forms of competition), and neither seed set nor population growth will necessarily be affected. The more pollen that is lost in the process of attracting and employing pollinators (e.g., to bees that collect pollen as well as pollinate), the more likely specialization is to evolve.

Because any shifts in pollination mode can lead to reproductive isolation, the diversifying selection caused by such competition may accelerate speciation and the diversification of angiosperm clades (Grant 1949; Johnson 2006; Kay and Sargent 2009; but see Armbruster and Muchhala 2009). For example, a subpopulation of a plant species adapted to one type of pollinator may disperse to a habitat where that pollinator frequently visits another plant. Selection on male function will then favor specializing on a different, underutilized pollinator in the new habitat, resulting in reproductive barriers between the subpopulations. Indeed, flowers are typically the first structures to change as angiosperm clades diversify, evidenced by the fact that plant taxonomists rely heavily on floral traits for species-level classification, and phylogenetic analyses of angiosperm groups often reveal frequent shifts between pollination modes (e.g., Armbruster 1993; Johnson et al. 1998; Whittall and Hodges 2007; Smith et al. 2008; Tripp and Manos 2008). We suggest that costs to male function modeled here have been an important factor driving such floral diversification.

Our study joins others in stressing the importance of community context in understanding the ecology and evolution of pollination systems (Moeller 2004; Strauss and Irwin 2004; Sargent and Ackerly 2008; Lazaro et al. 2009; Mitchell et al. 2009). If the plants in a community did not compete, all of them would be expected to converge on the most effective pollinator available in that habitat. However, our results show that for a given plant species, the

effectiveness of pollinators depends to a large degree on whether they are also visiting other species. In other words, even if two flower-visiting animals have identical characteristics, their effectiveness as pollinators can differ depending on the extent to which they are also visiting other plants in the community. Studies of pollinator effectiveness based solely on female fecundity (e.g., Motten et al. 1981; Armbruster and McGuire 1991; McGuire and Armbruster 1991; Dieringer 1992; Gomez and Zamora 1999; Mayfield et al. 2001; Sahli and Conner 2007; Blair and Williamson 2008; Madjidian et al. 2008) tend to miss this contextual effect.

Acknowledgments

We thank M. Rodríguez-Gironés and R. Sargent for comments on the manuscript and the Thomson Lab (J. Forrest, J. Manson, J. Ogilvie, A. Parker, and J. Thomson) for an insightful discussion of an earlier draft.

Literature Cited

- Aigner, P. A. 2001. Optimality modeling and fitness trade-offs: when should plants become pollinator specialists? *Oikos* 95:177–184.
- Armbruster, W. S. 1993. Evolution of plant pollination systems: hypotheses and tests with the Neotropical vine *Dalechampia*. *Evolution* 47:1480–1505.
- . 2006. Evolutionary and ecological aspects of specialized pollination: views from the arctic to the tropics. Pages 260–282 in N. M. Waser and J. Ollerton, eds. *Plant-pollinator interactions: from specialization to generalization*. University of Chicago Press, Chicago.
- Armbruster, W. S., and A. L. Herzig. 1984. Partitioning and sharing of pollinators by four sympatric species of *Dalechampia* (Euphorbiaceae) in Panama. *Annals of the Missouri Botanical Garden* 71: 1–16.
- Armbruster, W. S., and A. D. McGuire. 1991. Experimental assessment of reproductive interactions between sympatric *Aster* and *Erigeron* (Asteraceae) in interior Alaska. *American Journal of Botany* 78:1449–1457.
- Armbruster, W. S., and N. Muchhala. 2009. Associations between floral specialization and species diversity: cause, effect, or correlation? *Evolutionary Ecology* 23:159–179.
- Armbruster, W. S., M. E. Edwards, and E. M. Debevec. 1994. Floral character displacement generates assemblage structure of Western Australian triggerplants (*Stylidium*). *Ecology* 75:315–329.
- Bell, G. 1985. On the function of flowers. *Proceedings of the Royal Society B: Biological Sciences* 224:223–265.
- Blair, A. W., and P. S. Williamson. 2008. Effectiveness and importance of pollinators to the star cactus (*Astrophytum asterias*). *Southwestern Naturalist* 53:423–430.
- Brunet, J. 1992. Sex allocation in hermaphroditic plants. *Trends in Ecology & Evolution* 7:79–84.
- Campbell, D. R. 1985. Pollen and gene dispersal: the influences of competition for pollination. *Evolution* 39:418–431.
- Campbell, D. R., and A. F. Motten. 1985. The mechanism of competition for pollination between two forest herbs. *Ecology* 66:554–563.

- Caruso, C. M., and M. Alfaro. 2000. Interspecific pollen transfer as a mechanism of competition: effect of *Castilleja linariaefolia* pollen on seed set of *Ipomopsis aggregata*. *Canadian Journal of Botany* 78:600–606.
- Castellanos, M. C., P. Wilson, and J. D. Thomson. 2004. “Anti-bee” and “pro-bird” changes during the evolution of hummingbird pollination in *Penstemon* flowers. *Journal of Evolutionary Biology* 17:876–885.
- Charlesworth, D., and B. Charlesworth. 1981. Allocation of resources to male and female functions in hermaphrodites. *Biological Journal of the Linnean Society* 15:57–74.
- Charnov, E. L. 1979. Simultaneous hermaphroditism and sexual selection. *Proceedings of the National Academy of Sciences of the USA* 76:2480–2484.
- . 1982. *The theory of sex allocation*. Princeton University Press, Princeton, NJ.
- Conner, J. K. 1997. Floral evolution in wild radish: the roles of pollinators, natural selection, and genetic correlations among traits. *International Journal of Plant Sciences* 158(suppl.):S108–S120.
- Dieringer, G. 1992. Pollinator effectiveness and seed set in populations of *Agalinis strictifolia* (Scrophulariaceae). *American Journal of Botany* 79:1018–1023.
- Fenster, C. B., W. S. Armbruster, P. Wilson, M. R. Dudash, and J. D. Thomson. 2004. Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution, and Systematics* 35:375–403.
- Flanagan, R. J., R. J. Mitchell, D. Knutowski, and J. D. Karron. 2009. Interspecific pollinator movements reduce pollen deposition and seed production in *Mimulus ringens* (Phrymaceae). *American Journal of Botany* 96:809–815.
- Forrest, J., and J. D. Thomson. 2009. Background complexity affects colour preference in bumblebees. *Naturwissenschaften* 96:921–925.
- Futuyma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. *Annual Review of Ecology and Systematics* 19:207–233.
- Gomez, J. M., and R. Zamora. 1999. Generalization vs. specialization in the pollination system of *Hormathophylla spinosa* (Cruciferae). *Ecology* 80:796–805.
- . 2006. Ecological factors that promote the evolution of generalization in pollination systems. Pages 145–166 in N. M. Waser and J. Ollerton, eds. *Plant-pollinator interactions: from specialization to generalization*. University of Chicago Press, Chicago.
- Grant, V. 1949. Pollination systems as isolating mechanisms in angiosperms. *Evolution* 3:82–97.
- Harder, L. D. 2000. Pollen dispersal and the floral diversity of monocotyledons. Pages 243–257 in K. L. Wilson and D. Morris, eds. *Monocots: systematics and evolution*. CSIRO, Melbourne.
- Harder, L. D., and M. B. Routley. 2006. Pollen and ovule fates and reproductive performance by flowering plants. Pages 61–80 in L. D. Harder and S. C. H. Barrett, eds. *Ecology and evolution of flowers*. Oxford University Press, Oxford.
- Hodges, S. A., and M. L. Arnold. 1995. Spurring plant diversification: are floral nectar spurs a key innovation? *Proceedings of the Royal Society B: Biological Sciences* 262:343–348.
- Irwin, R. E., and A. K. Brody. 2000. Consequences of nectar robbing for realized male function in a hummingbird-pollinated plant. *Ecology* 81:2637–2643.
- Johnson, S. D. 2006. Pollinator-driven speciation in plants. Pages 296–306 in L. D. Harder and S. C. H. Barrett, eds. *The ecology and evolution of flowers*. Oxford University Press, Oxford.
- Johnson, S. D., and K. E. Steiner. 2000. Generalization versus specialization in plant pollination systems. *Trends in Ecology & Evolution* 15:140–143.
- Johnson, S. D., L. F. Delph, and C. L. Elderkin. 1995. The effect of petal-size manipulation on pollen removal, seed set, and insect-visitor behavior in *Campanula americana*. *Oecologia (Berlin)* 102:174–179.
- Johnson, S. D., H. P. Linder, and K. E. Steiner. 1998. Phylogeny and radiation of the pollination systems in *Disa* (Orchidaceae). *American Journal of Botany* 85:402–411.
- Johnson, S. D., P. R. Neal, and L. D. Harder. 2005. Pollen fates and the limits on male reproductive success in an orchid population. *Biological Journal of the Linnean Society* 86:175–190.
- Johnson, S. D., A. L. Hargreaves, and M. Brown. 2006. Dark, bitter-tasting nectar functions as a filter of flower visitors in a bird-pollinated plant. *Ecology* 87:2709–2716.
- Kay, K. M., and R. D. Sargent. 2009. The role of animal pollinators in plant speciation: integrating ecology, geography, and genetics. *Annual Review of Ecology, Evolution, and Systematics* 40:637–656.
- Kay, K. M., C. Voelckel, J. Y. Yang, K. M. Hufford, D. D. Kaska, and S. A. Hodges. 2006. Floral characters and species diversification. Pages 311–325 in L. D. Harder and S. C. H. Barrett, eds. *Ecology and evolution of flowers*. Oxford University Press, Oxford.
- Kessler, D., G. Klaus, and I. T. Baldwin. 2008. Field experiments with transformed plants reveal the sense of floral scents. *Science* 321:1200–1202.
- Kiester, A. R., R. Lande, and D. W. Schemske. 1984. Models of coevolution and speciation in plants and their pollinators. *American Naturalist* 124:220–243.
- Knight, T. M., J. A. Steets, J. C. Vamosi, S. J. Mazer, M. Burd, D. R. Campbell, M. R. Dudash, M. Johnston, R. J. Mitchell, and T.-L. Ashman. 2005. Pollen limitation of plant reproduction: pattern and process. *Annual Review of Ecology, Evolution, and Systematics* 36:467–497.
- Kudo, G., and L. D. Harder. 2005. Floral and inflorescence effects on variation in pollen removal and seed production among six legume species. *Functional Ecology* 19:245–254.
- Kwak, M. M., and O. Jennersten. 1991. Bumblebee visitation and seed set in *Melampyrum pratense* and *Viscaria vulgaris*: heterospecific pollen and pollen limitation. *Oecologia (Berlin)* 86:99–104.
- Lau, J. A., R. E. Miller, and M. D. Rausher. 2008. Selection through male function favors smaller floral display size in the common morning glory *Ipomoea purpurea* (Convolvulaceae). *American Naturalist* 172:63–74.
- Lazaro, A., R. Lundgren, and O. Totland. 2009. Co-flowering neighbors influence the diversity and identity of pollinator groups visiting plant species. *Oikos* 118:691–702.
- Levin, D. A., and W. W. Anderson. 1970. Competition for pollinators between simultaneously flowering species. *American Naturalist* 104:455–467.
- Lloyd, D. G. 1984. Gender allocations in outcrossing cosexual plants. Pages 277–300 in R. Dirzo and J. Sarukhán, eds. *Perspectives in plant population ecology*. Sinauer, Sunderland, MA.
- Madjidian, J. A., C. L. Morales, and H. G. Smith. 2008. Displacement of a native by an alien bumblebee: lower pollinator efficiency

- overcome by overwhelmingly higher visitation frequency. *Oecologia* (Berlin) 156:835–845.
- Martén-Rodríguez, S., A. Almarales-Castro, and C. B. Fenster. 2009. Evaluation of pollination syndromes in Antillean Gesneriaceae: evidence for bat, hummingbird and generalized flowers. *Journal of Ecology* 97:348–359.
- Mayfield, M. M., N. M. Waser, and M. V. Price. 2001. Exploring the “most effective pollinator principle” with complex flowers: bumblebees and *Ipomopsis aggregata*. *Annals of Botany* 88:591–596.
- Maynard Smith, J. 1971. The origin and maintenance of sex. Pages 163–175 in G. C. Williams, ed. *Group selection*. Aldine Atherton, Chicago.
- McGuire, A. D., and W. S. Armbruster. 1991. An experimental test for reproductive interactions between two sequentially blooming *Saxifraga* species (Saxifragaceae). *American Journal of Botany* 78: 214–219.
- Mitchell, R. J., R. J. Flanagan, B. J. Brown, N. M. Waser, and J. D. Karron. 2009. New frontiers in competition for pollination. *Annals of Botany* 103:1403–1413.
- Moeller, D. A. 2004. Facilitative interactions among plants via shared pollinators. *Ecology* 85:3289–3301.
- Montgomery, B. R. 2009. Do pollen carryover and pollinator constancy mitigate effects of competition for pollination? *Oikos* 118: 1084–1092.
- Morales, C. L., and A. Traveset. 2008. Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. *Critical Reviews in Plant Sciences* 27:221–238.
- Morgan, M. T. 1992. The evolution of traits influencing male and female fertility in outcrossing plants. *American Naturalist* 139: 1022–1051.
- Motten, A. F., D. R. Campbell, D. E. Alexander, and H. L. Miller. 1981. Pollination effectiveness of specialist and generalist visitors to a North Carolina population of *Claytonia virginica*. *Ecology* 62: 1278–1287.
- Muchhala, N. 2003. Exploring the boundary between pollination syndromes: bats and hummingbirds as pollinators of *Burmeistera cyclostigmata* and *B. tenuiflora*. *Oecologia* (Berlin) 134:373–380.
- . 2007. Adaptive trade-off in floral morphology mediates specialization for flowers pollinated by bats and hummingbirds. *American Naturalist* 169:494–504.
- Muchhala, N., and M. D. Potts. 2007. Character displacement among bat-pollinated flowers of the genus *Burmeistera*: analysis of mechanism, process and pattern. *Proceedings of the Royal Society B: Biological Sciences* 274:2731–2737.
- Murcia, C., and P. Feinsinger. 1996. Interspecific pollen loss by hummingbirds visiting flower mixtures: effects of floral architecture. *Ecology* 77:550–560.
- Pijl, L. 1961. Ecological aspects of flower evolution. II. Zoophilous flower classes. *Evolution* 15:44–59.
- Rathcke, B. J. 1983. Competition and facilitation among plants for pollination. Pages 305–329 in L. Real, ed. *Pollination biology*. Academic Press, New York.
- Ree, R. H. 2005. Detecting the historical signature of key innovations using stochastic models of character evolution and cladogenesis. *Evolution* 59:257–265.
- Rodríguez-Gironés, M. A., and A. L. Llandres. 2008. Resource competition triggers the co-evolution of long tongues and deep corolla tubes. *PLoS ONE* 3:e2992.
- Rodríguez-Gironés, M. A., and L. Santamaría. 2005. Resource partitioning among flower visitors and evolution of nectar concealment in multi-species communities. *Proceedings of the Royal Society B: Biological Sciences* 272:187–192.
- . 2007. Resource competition, character displacement, and the evolution of deep corolla tubes. *American Naturalist* 170:455–464.
- Rush, S., J. K. Conner, and P. Jenetten. 1995. The effects of natural variation in pollinator visitation on rates of pollen removal in wild radish, *Raphanus raphanistrum* (Brassicaceae). *American Journal of Botany* 82:1522–1526.
- Sahli, H. F., and J. K. Conner. 2007. Visitation, effectiveness, and efficiency of 15 genera of visitors to wild radish, *Raphanus raphanistrum* (Brassicaceae). *American Journal of Botany* 94:203–209.
- Sargent, R. D. 2004. Floral symmetry affects speciation rates in angiosperms. *Proceedings of the Royal Society B: Biological Sciences* 271:603–608.
- Sargent, R. D., and D. D. Ackerly. 2008. Plant-pollinator interactions and the assembly of plant communities. *Trends in Ecology & Evolution* 23:123–130.
- Sargent, R. D., and S. P. Otto. 2006. The role of local species abundance in the evolution of pollinator attraction in flowering plants. *American Naturalist* 167:67–80.
- Schiestl, F. P., and P. M. Schluter. 2009. Floral isolation, specialized pollination, and pollinator behavior in orchids. *Annual Review of Entomology* 54:425–446.
- Schluter, D. 2000. Ecological character displacement in adaptive radiation. *American Naturalist* 156(suppl.):S4–S16.
- Schoen, D. J., and T.-L. Ashman. 1995. The evolution of floral longevity: resource-allocation to maintenance versus construction of repeated parts in modular organisms. *Evolution* 49:131–139.
- Shuttleworth, A., and S. D. Johnson. 2009. The importance of scent and nectar filters in a specialized wasp-pollination system. *Functional Ecology* 23:931–940.
- Smith, S. D., C. Ane, and D. A. Baum. 2008. The role of pollinator shifts in the floral diversification of *Iochroma* (Solanaceae). *Evolution* 62:793–806.
- Stanton, M., H. J. Young, N. C. Ellstrand, and J. M. Clegg. 1991. Consequences of floral variation for male and female reproduction in experimental populations of wild radish, *Raphanus sativus* L. *Evolution* 45:268–280.
- Stebbins, G. L. 1970. Adaptive radiation of reproductive characteristics in angiosperms. I. Pollination mechanisms. *Annual Review of Ecology and Systematics* 1:307–326.
- Stone, G. N., P. Willmer, and J. A. Rowe. 1998. Partitioning of pollinators during flowering in an African *Acacia* community. *Ecology* 79:2808–2827.
- Strauss, S. Y., and R. E. Irwin. 2004. Ecological and evolutionary consequences of multispecies plant-animal interactions. *Annual Review of Ecology, Evolution, and Systematics* 35:435–466.
- Strauss, S. Y., J. K. Conner, and K. P. Lehtila. 2001. Effects of foliar herbivory by insects on the fitness of *Raphanus raphanistrum*: damage can increase male fitness. *American Naturalist* 158:496–504.
- Thomson, J. D. 2003. When is it mutualism? *American Naturalist* 162(suppl.):S1–S9.
- Thomson, J. D., B. J. Andrews, and R. C. Plowright. 1981. The effect of foreign pollen on ovule development in *Diervilla lonicera* (Caprifoliaceae). *New Phytologist* 90:777–783.
- Tripp, E. A., and P. S. Manos. 2008. Is floral specialization an evo-

- lutionary dead-end? pollination system transitions in *Ruellia* (Acanthaceae). *Evolution* 62:1712–1737.
- Vaughton, G., and M. Ramsey. 1998. Floral display, pollinator visitation and reproductive success in the dioecious perennial herb *Wurmbea dioica* (Liliaceae). *Oecologia* (Berlin) 115:93–101.
- Waser, N. M. 1983. Competition for pollination and floral character differences among sympatric plant species: a review of the evidence. Pages 277–293 in C. E. Jones and R. J. Little, eds. *Handbook of experimental pollination biology*. Van Nostrand Reinhold, New York.
- Waser, N. M., and M. L. Fugate. 1986. Pollen precedence and stigma closure: a mechanism of competition for pollination between *Delphinium nelsonii* and *Ipomopsis aggregata*. *Oecologia* (Berlin) 70: 573–577.
- Waser, N. M., L. Chittka, M. V. Price, N. M. Williams, and J. Ollerton. 1996. Generalization in pollination systems, and why it matters. *Ecology* 77:1043–1060.
- Whittall, J. B., and S. A. Hodges. 2007. Pollinator shifts drive increasingly long nectar spurs in columbine flowers. *Nature* 447: 706–710.
- Wilson, P., and J. D. Thomson. 1996. How do flowers diverge? Pages 88–111 in D. G. Lloyd and S. C. H. Barrett, eds. *Floral biology: studies on floral evolution in animal-pollinated plants*. Chapman & Hall, New York.
- Associate Editor: Christopher G. Eckert
Editor: Mark A. McPeck



A flower of *Burmeistera glabrata* being visited by a nectar bat (*Anoura cultrata*) with pollen under its wing from a recent visit to a different species (*Marcgravia* sp.). Photograph by Nathan Muchhala.