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How Do Flowers Diverge?

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> Two populations of the same plant species living in different territories may both receive effective pollination visits from the same two classes of pollinators, say bees and beeflies, but receive the two types of visitations in different relative frequencies. If one local race receives a greater number of effective bee visits and the other population a greater number of effective beefly visits, natural selection will favor closer floral adaptations to the special characteristics of bees in the first race and closer coadaptations with beeflies in the second. The point of compromise in floral adaptations will shift in correspondence with the climate of pollinators in each given territory.
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> —V. and K.A. Grant (1965)

Evolutionary Thought and Floral Biology

Darwin's orchid book (1862) has been cited as his first detailed example of how to study evolution (Ghiselin, 1969; Gould, 1986). The book starts as a presentation of observations showing that the morphology of orchids is, in most cases, wonderfully well suited to having insects remove and deposit pollinia. It ends by tracing how the enormous diversity of orchids can be seen as arising through modifications from ancestral forms. What Darwin did not do was to explain how orchid flowers come to be different. He probably thought that by showing how to study the origin of adaptation he had shown how to study the origin of diversity. Mayr has often pointed out that Darwin failed to see genetic isolation as a precondition for speciation, and thus for diversification (e.g., Mayr, 1959). Likewise, we contend that evolutionists have seldom clearly dissected the alternatives for how divergence occurs, given isolation. We shall concern ourselves here with how different environments—in our case, different pollinator regimes—do or do not provide heterogeneity in selection that might adaptively drive the divergence of flowers.

Before the neo-Darwinian synthesis, it was common for biologists to argue that the distinguishing characters of closely related species are often nonadaptive (Provine, 1986). Richards and Robson (1926) provided the most influential review, arguing forcefully that there are many contrasts for which stories about special adaptations had simply not been proven. Their perspective was thoughtfully adopted by Elton (1927). On the one hand, Elton imagined that the minor

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characters distinguishing geographical races, subspecies, and species are not due to selection in different environments, but rather spread through fluctuations in population size (Elton's Chap. XII). And, on the other hand, Elton believed that organisms are elegantly adapted to niches such that badgers and weasels end up filling different roles in the structure of their community (Elton's Chap. V). Our reading of Elton is that he was thinking of two scales of evolutionary differentiation, and that his interpretation of neutrality vs. selection is scale-dependent (Elton, p. 185). This is a point that we will return to at the end of our chapter when reviewing the many ways by which flowers might diverge.

At the beginning of the neo-Darwinian synthesis, Dobzhansky (1937) and the other masters of the synthesis did not insist on the adaptive nature of species differences (Gould, 1983). Stebbins (1950) had his adaptationist leanings, but still admitted he could not fully back them up for floral characters (pp. 118–121). But, as the synthesis hardened and MacArthurian ecology was born (MacArthur, 1958, 1972), the celebration of pervasive adaptation spread to an almost consensus view (e.g., Lack 1971). It seemed as if every species of animal claimed for itself its own niche unlike the niche of any other (coexisting) animal. A naive extension to plants would suggest that each flower is adapted to a pollination niche unique in its community.

In fact, floral biology did not walk lock step with zoological thought, but there was a loose connection. During the third quarter of this century, much work was done on flowers from the perspective of comparative functional morphology (Vogel, 1954; Baker, 1961; van der Pijl, 1961). The classic example was Grant and Grant's (1965) exploration of adaptive radiation in the phlox family. The data of that period generally consisted of observing what species of animals visit various kinds of flowers, how the visitors behave at the flowers, and whether or not they come into bodily contact with anthers and stigmas. The results were that different types of flowers attract different types of visitors, that flowers have many features used by their particular visitors, and that only some visitors are effective pollinators. Floral differences came to be treated as adaptations to diverse pollinator communities. This conclusion was based on broad-scale comparisons between flowers pollinated by butterflies vs. bees vs. bats vs. birds. Although there was an implication that differences between species pollinated by the same general type of animal are also adaptive, this now seems mostly like an extrapolation down from the major products of evolution. It assumes that floral divergence, whether fine or coarse in scale, is uniformly driven by one set of evolutionary mechanisms.

Floral syndromes as adaptations to fixed pollinator types have a certain typological ring about them that made the concept distasteful to a new generation of pollination biologists in the late 1970s. Trained in ecology rather than systematics, they emphasized community-level interactions such as competition and facilitation (Brown and Kodric-Brown, 1979). In these interactions, they saw not only rules for community assembly based on limiting similarity, but also a mechanism for the potent selection of floral attributes via niche partitioning and character displacement (Waser, 1978, 1983*a;* Pleasants, 1980, 1983; Thomson, 1978, 1982; Nilsson, 1983). The distinction between population-dynamic processes and character evolution was often blurred, and certain aspects of flowers, such as nectar production and phenological timing, were considered to be more responsive to community influences than floral morphology (see Zimmerman, 1988). These researchers' faith in their ability to comprehend floral evolution was soon shaken by a series of realizations—by the null-model revolution in community ecology (Rabinowitz et al., 1981; Strong et al., 1979, 1984), by the onerous burden of verifying character displacement (Grant, 1972), by criticisms of Panglossian adaptationism (Gould and Lewontin, 1979; Waser, 1983*b*), by the comprehension that the results of competition experiments can have many interpretations (Thomson, 1980; Bender et al., 1984), and by numerous complications that their own studies revealed. Plant-pollinator communities came to look less equilibrial, more dominated by spatio-temporal heterogeneity, historical influences, and convoluted species interactions (Feinsinger, 1987).

Many plant reproductive ecologists responded by turning toward processes that act within populations, trying to supply the details of genetics and the mechanisms of selection whose absence had crippled earlier arguments. With a few exceptions, such as Armbruster (e.g., 1988 and Chapter 9), they stopped working on diversification *per se*. Much of the recent work has focused on *how* natural selection acts on floral characters in a single population (Waser and Price, 1983; Nilsson, 1988; Campbell, 1989; Stanton et al., 1989; Galen, 1989; Schemske and Horvitz, 1989; Devlin et al., 1992; Mitchell, 1993; Chapters 10 and 11). This work tends to be more reductionistic and empirically demanding than previous work. A field that once freely indulged in ornate adaptive speculation now wishes for measurements of lifetime reproductive success through both male and female function.

One approach to estimating components of male and female function has been to focus on the rates of pollen removal from anthers and pollen delivery to stigmas. Pollen grains are small, numerous, and difficult to track, but new techniques have allowed for some quantitative study of their dispersal (Stanton et al., 1992). With simplifying assumptions, pollen-transfer parameters can be treated as surrogates of fitness (e.g., Thomson and Thomson, 1989), and some progress has now been made in understanding what influences how much pollen is dispersed by pollinators (Harder et al., 1985; Galen and Stanton, 1989; Harder and Thomson, 1989; Young and Stanton, 1990; Harder, 1990; Wilson and Thomson, 1991; Harder and Barrett, 1993; Chapter 6). Efficient new techniques now let us measure pollen removal and pollen deposition for large samples of flowers. By controlling or noting the species of pollinator and controlling or measuring the morphology of flowers, we can then use statistical procedures to examine the influence of pollinator-species variation, floral-morphological variation, and the interaction between the two in determining how much pollen is dispersed. We believe this interaction is of particular interest in understanding the origin of the sorts of floral differences that distinguish closely related plants pollinated by similar types of animals.

Why the Interaction Term Is Important

In 1984, Schemske and Horvitz entitled one of their papers, "Variation among floral visitors in pollination ability: A precondition for mutualism specialization." To provide an example of such variation, they presented data showing that bees are better than butterflies at tripping *Calathea* flowers, and they stressed that adaptation to one pollinator over another is driven by such differences in the average effectiveness of pollinators. A similar focus on overall (i.e., average) differences in effectiveness had been made previously by Primack and Silander (1975) and has been repeated subsequently by Herrera (1987). Schemske and Horvitz alluded to something else also: "In view of the variation in the pollination ability of different visitors, the reproductive success of individual plants is a function of plant characters that determine the number and kinds of visitors that a plant attracts. The extent to which variation in plant fitness is attributable to such characters determines the potential for selection of pollinators on plants." We extend this to mean that, in order for specialization to occur, visitors must differ not only in their overall quality, but also in the way they affect the relationship between floral traits and fitness.

We are interested in the visitor species × floral character interaction term, in other words, in the way different animals affect selection gradients with differing slopes (Wade and Kalisz, 1990). By selection gradient, we mean the relationship between some measure of fitness and a character. Strictly speaking, it is the standardized partial regression of fitness on a character, as it naturally varies, holding other characters constant, and it is considered a measure of the direct action of selection on a focal character (Lande and Arnold, 1983). Our usage, however, will be fairly loose in that we will treat pollen counts as fitness, and we will not present standarized coefficients. Our aim is simply to look for any evidence that different bees might affect selection on flowers differently.

Specialization can occur when there is variation in floral characters that can effectively limit the impact of inferior types of visitors while promoting pollination by superior visitors. Consider Fig. 4.1 and imagine we are at a site where Bees A and B occur. With either of the bees, flowers having shorter corollas work better than those with longer corollas. The two bee species differ in their means—Bee B is a relative parasite compared to Bee A—but still the flowers will evolve toward shorter corollas and still they will be visited by Bee B. Now, imagine we are at a site with Bees B and C. These bees affect selection gradients in opposite directions, and because Bee C is the better pollinator, the flowers will evolve to be specialized on Bee C by an increase in corolla length. In a

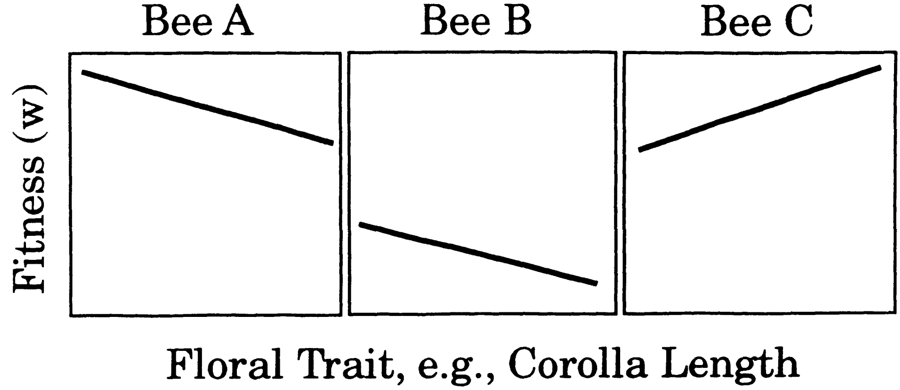

Figure 4.1. Various relationships between floral morphology and fitness, as determined by different hypothetical bee species. Bee A differs from bee B in its *average* effect on fitness. Bee A differs from bee C in the *slopes* of its effect.

single place inhabited by Bees A and C, Schemske and Horvitz are right in saying that there will be no specialization because A and C are effectively the same.

However, because we are concerned with the origin of divergence, we wish to consider a series of isolated plant populations visited by various admixtures of bees, but with one bee species more or less predominating at any one site. Where Bee A predominates, the corolla tubes will evolve to be shorter. Where Bee C predominates, the corollas will evolve to be longer. Where Bee B exists in the virtual absence of the other two, corollas will become shorter, but if Bee A is present in secondary abundance, the flowers will still evolve under A's influence (following "the most-important pollinator principle" of Stebbins, 1970). Thus, the contrast that most clearly leads to adaptive divergence is between sites dominated by A vs. C: The pollinators impose opposite selection gradients (slopes) but are actually comparable in their overall quality (means). It is this crucial interaction term—visitor species × floral attribute, or more generally, environment × character—that we wish to examine as a first step in reattacking the nature of divergence. Here we present two studies of wildflowers pollinated by bumble bees, both of which allowed us to evaluate such interaction terms. We did not try to locate actual populations served by different suites of pollinators, but we did examine pollen removal and deposition in single visits by different species of bumble bees to flowers that exhibited natural character variation.

Jewelweed Study

Impatiens pallida (Balsaminaceae) has gullet-shaped protandrous flowers (Fig. 4.2). The gender phases are absolutely distinct in that the androecium completely

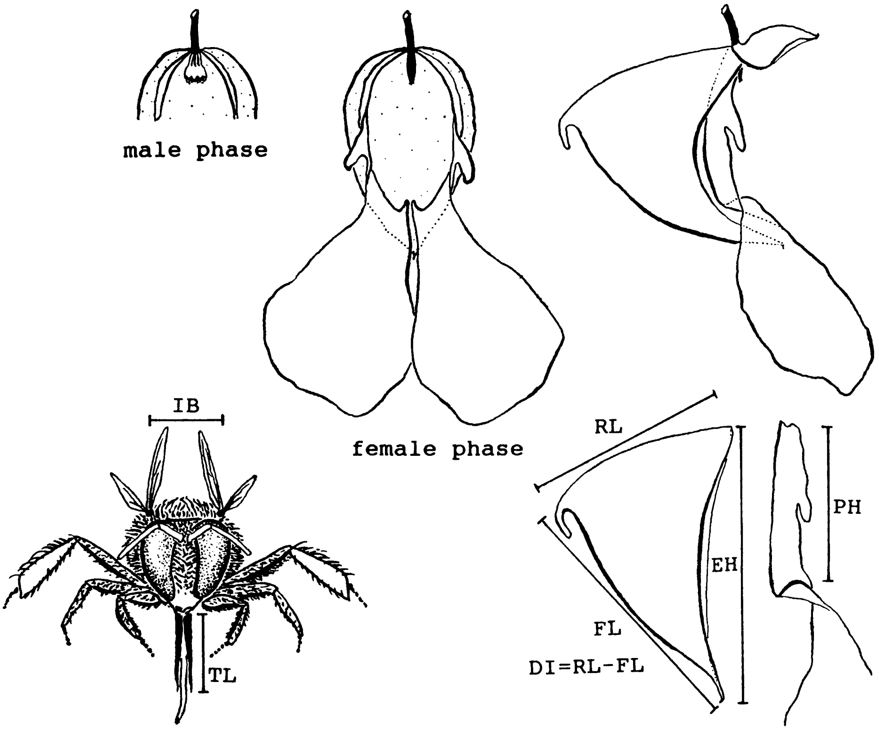

Figure 4.2. *Impatiens pallida* and *Bombus impatiens* showing how measurements were taken. Notice that the flowers fit around the bees quite snugly.

covers the gynoecium until the gynoecium swells and pushes the androecium away; thus, both the androecium and gynoecium are presented in the same place, pointing down from the roof of the vestibular sepal. The male phase is somewhat longer than the female phase (Schemske, 1978). Local populations are remarkably differentiated in morphology and in the plants' ability to grow and reproduce (Schemske, 1984), and in one population in Quebec, phenotypic selection on plant size and phenology was found to be strong and spatially heterogeneous (Stewart and Schoen, 1987). *Impatiens* flowers are visited by a variety of animals but are as clearly adapted to bumble bee pollination as any flower. Bee activity varies from nil (rarely) to hundreds of visits (often) during the life of a flower. Bees crawl into the vestibular sepal in order to drink nectar from a recurved spur, and in the process their backs brush against the androecium or the stigma. While foraging, bees develop an obvious stripe of white pollen that runs down their backs. The fit between bee and flower can be snug, and one would expect that bee size and flower size could strongly influence pollen removal and deposition.

Methods

We were interested in how much pollen is removed from anthers and deposited on stigmas in a visit. Since pollen removal is not directly measurable, we counted the number of grains *not* removed, which can be treated as the opposite of removal or used to calculate removal by subtracting from the amount of pollen produced in unvisited control flowers. Our two surrogates of fitness, then, were pollen remaining in anthers and pollen deposited on stigmas in a single visit. It is hard to know how these variables are related to reproductive success (Snow, 1989; Wilson and Thomson, 1991; Stanton et al., 1992). High pollen removal may be either negatively or positively correlated with male reproductive success, depending on how much of the removed pollen is taken to stigmas, and on whether or not the pollen that is not removed in one visit is later removed and subsequently deposited in another visit (Harder and Thomson, 1989). High pollen deposition may be correlated with high female reproductive success, but only when seed set or progeny quality is visitor-limited (Wilson et al., 1994). Still, pollen removal and deposition are necessary for reproduction and must be in some way related to reproductive success. Moreover, they have the advantage of being the variables that bees most directly affect, and so, of all surrogates of fitness, they should be the most deterministic and statistically tractable. If neither removal nor deposition were related to pollination variation, it is hard to imagine how fitness could be.

During August of 1990, *Impatiens pallida* flowers were covered by wax paper bags, in bud or in male phase. Overnight, the buds matured into virgin male-phase flowers, and the previously male-phase flowers matured into virgin female-phase flowers. Each flower, except for unvisited controls, was cut and put in a florist's cut-flower holder taped to the end of a stick, where it was presented to a naturally foraging *Bombus* worker for a single visit. The visit was timed with a stopwatch. *Bombus vagans, B. impatiens, B. fervidus,* and unvisited control treatments were administered in roughly rotating order (except that additional *B. vagans*-visited flowers, taken for other purposes, are here included in the data). For male-phase flowers, the androecium was carefully detached, placed in a microcentrifuge tube, and preserved in 70% ethanol. For female-phase flowers, the stigma was clipped, placed on a microscope slide with a small piece of fuchsin-tinted glycerin jelly, heated with an alcohol burner, and squashed under a cover slip. The rest of the flower was put in a plastic vial and preserved in ethanol.

Flowers were measured in random order under a dissecting microscope while being floated in alcohol over 1 mm graph paper. Measurements were precise to about 0.2 mm. Three floral characters will be reported on here and are illustrated in Fig. 4.2: the entrance height (EH) of the vestibule when gently flattened, the porch height (PH) of a flattened petal, and the difference (DI) between the length of the floor and the roof of the vestibule. We imagined that an increase in any of these characters might have led to less contact between the bee and the androecium or stigma and therefore less pollen moved. Such a relationship could also have been expected to itself vary with bees of differing sizes. The number of pollen grains left in androecia was estimated using an Elzone® electronic particle counter with a 76 μ aperture (Harder, 1990). Pollen deposited on stigmas was determined using a compound microscope with an ocular grid and mechanical stage.

Results

The three *Bombus* species differed considerably in overall size, tongue length, and the duration of their visits (Table 4.1). *Bombus vagans* was the smallest, *B. impatiens* intermediate, and *B. fervidus* the largest, as indexed by the distance between the bases of the wings. Tongue lengths did not correspond to body size in that the order was *B. impatiens* with the shortest tongue, followed by *B. vagans,* and *B. fervidus*. Probably because of its greater tongue length, *B. fervidus* did not crawl into the flowers as deeply as the smaller species and may have fit more loosely despite its greater size. *Bombus vagans* spent the most time at a flower, *B. impatiens* less, and *B. fervidus* the least time. Pollen removal and deposition were not significantly related to visit duration (statistics not shown).

Both pollen remaining in androecia (our measure of pollen removal) and the log of pollen deposited on stigmas have approximately normal distributions. Table 4.2 shows a series of progressively simpler statistical models by which we tried to explain variance in the amount of pollen remaining and the log of pollen deposition. In the full models, shown in the top panel, only 17 and 11%

Table 4.1. Comparisons of three bee species: morphometrics, visit length, and effects on pollen movement in one visit to flowers of Impatiens pallida. *Numbers are means ± standard errors (sample sizes).*

	B. vagans	*B. impatiens*	*B. fervidus*
Distance between wing bases (mm)	3.47±0.130(8)	3.74±0.082(8)	4.35±0.141(6)
Tongue length (mm)	4.46±0.161(8)	3.73±0.103(8)	5.89±0.090(6)
Duration of visit (sec)*	20 at ♂, 10 at ♀	16 at ♂, 8 at ♀	8 at ♂, 6 at ♀
Pollen remaining (grains)†	474,000±22,300(53)	511,000±20,500(39)	520,000±21,100(38)
Log (pollen deposited + 1)‡	2.517±0.0499(67)	2.680±0.0660(35)	2.576±0.0536(43)
= back transformed value	= 328 grains	= 478 grains	= 376 grains

*The distribution of durations was very skewed so the geometric mean was calculated; standard errors are not presented.

†There were on average 707,000±17,200(46) grains produced in unvisited flowers; the number removed could be calculated by subtraction.

‡There were a very few pollen grains on stigmas of unvisited flowers: 0.415±0.0540(41) = 1.6 grains.

Table 4.2. Analyses of variance (bottom), covariance (middle), and heterogeneity in slopes (top) for pollen remaining and pollen deposited in a single visit of one of three Bombus *species to flowers of* Impatiens pallida. *Unvisited control flowers are not included in the analysis. EH, PH, and DI are measurements of the flowers that might have affected how tightly they fit around bees and thus how much pollen was moved. Three successively simpler models are presented for each variable. The difference between the top model and middle model represents the effect of the bee-species × floral-morphology interaction, which was not significant for either removal or deposition (see text) despite the marginal significance of bee species × DI.*

	Pollen in Androecium			Log (Pollen Deposited + 1)		
	df	III-SS[1]	*F*	df	III-SS	*F*
Bee species	2	143		2	0.437	
EH	1	791		1	0.002	
PH	1	921		1	0.042	
DI	1	178		1	0.063	
Bee × EH	2	397	1.05 n.s.	2	0.559	1.90 n.s.
Bee × PH	2	43	<1 n.s.	2	0.044	<n.s.
Bee × DI	2	1175	3.12*	2	0.202	<1 n.s.
Model	11	4525	$R^2=0.17$	11	2.424	$R^2=0.11$
Error	118	22,244		133	19.596	
Bee species	2	618	1.61 n.s.	2	0.684	2.24 n.s.
EH	1	779	4.05*	1	0.019	<1 n.s.
PH	1	1009	5.25*	1	0.041	<0.1 n.s.
DI	1	104	<1 n.s.	1	0.084	<1 n.s.
Model	5	2921	$R^2=0.11$	5	0.783	$R^2=0.04$
Error	124	26,768		139	21.021	
Bee species	2	545	1.32 n.s.	2	0.612	2.03 n.s.
Error	127	26,223	$R^2=0.02$	142	21.408	$R^2=0.03$

*Type III sums of squares × 100,000,000.

n.s. $p>0.1$.

*$p<0.05$.

of the variances, respectively, were explained. The interaction between bee species and the three dimensions was not significant except for bee species × DI for pollen remaining ($p = 0.048$): DI was positively related to pollen remaining for *B. vagans* and *B. fervidus,* but negatively related for *B. impatiens.* If we drop the three interaction terms and calculate the decreases in the models' degrees of freedom and sums of squares, then we can evaluate the collective significance of those interaction terms. For pollen remaining, SS = 1604 and $F_{6,118} = 1.42$; for pollen deposited, SS = 1.641 and $F_{6,133} = 1.86$. Neither was significant.

As shown in the simplified models in the middle of Table 4.2, EH and PH had a significant effect on pollen removal (or possibly they were correlated with pollen production, although this was not evident among the unvisited control flowers; Wilson, in press). There did not seem to be any effect of EH, PH, or

Table 4.3. Comparisons of two bee species: size, visit length, and effects on pollen movement in one visit to flowers of Erythronium grandiflorum. *Numbers are means ± standard errors (samples sizes).*

	Bombus occidentalis	*Bombus bifarius*
Distance between wing bases (mm)	7.09±0.095(8)	5.92±0.081(8)
Duration of visit (sec)[1]	21	16
Pollen remaining (grains)	25,900±1730(76)	31,700±1640(79)
Pollen deposited (grains)	1791±104.5(76)	988±54.2(78)

[1] Visit durations were skewed so the geometric mean was calculated and standard errors are not presented.

DI on pollen deposited (Table 4.2, middle panel). The collective effect of floral morphology was likewise significant for pollen remaining (SS = 2376; $F_{3,124} = 3.67$) and not significant for pollen deposited (SS = 0.171; $F_{3,139} < 1$).

Finally, as shown in the bottom panel of Table 4.2, bee species by itself had no affect on pollen remaining or pollen deposited. Bees did remove and deposit pollen, but the three *Bombus* species did so in comparable amounts (Table 4.1).

Glacier Lily Study

Erythronium grandiflorum (Liliaceae) has large open pendant flowers (Fig. 4.3). It is visited primarily by queen bumble bees with occasional visits by hummingbirds and small bees. Fair-weather visitation rates are a bit less than one visit per flower per day, and flowers last for about 4 to 5 days (Thomson and Thomson,

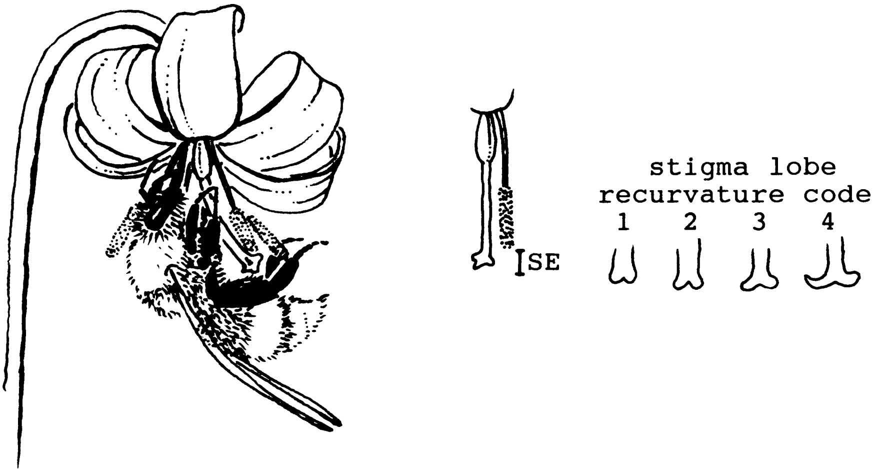

Figure 4.3. Erythronium grandiflorum and *Bombus occidentalis*. Stigma exsertion (SE) varies quite considerably and affects the amount of pollen that gets deposited on a visit.

1992). Bumble bees forage exclusively for nectar, which is produced at the base of the tepals. Pollen is incidentally removed from the six dangling anthers, and on flights between flowers, bees groom off pollen and discard it (Thomson, 1986). Stigmas vary from being exserted up to 5 mm beyond the anther tips to being included 2 mm behind them (Thomson and Stratton, 1985). Thomson (1986) previously suggested that small *Bombus* frequently fail to contact stigma. Here we were interested in how pollen transfer is related to stigma exsertion, bee species, and most importantly to the interaction between them.

Methods

We studied pollen removal and deposition in flowers of *Erythronium grandiflorum,* comparing queens of *Bombus occidentalis* and *B. bifarius,* the most important pollinators in the subalpine meadows of western Colorado where we did the work. We picked buds that had begun to open, placed them indoors in florists' cut-flower holders, and measured with calipers the length of the longest anther before any anthers had begun to dehisce. It was already known that anther length is linearly related to pollen production (Thomson and Thomson, 1989). Within 1 to 2 days, flowers typically had opened completely, all six anthers had dehisced, and stigmas were receptive with well-developed papillae.

We caught bees on *Erythronium grandiflorum* or *Taraxacum officinale*. In the latter case, we enclosed the bees in flight cages with large numbers of *E. grandiflorum* flowers for at least 2 days, so that they became proficient visitors before being tested. For testing, we would enclose a chilled bee in a flight cage with about 20 measured flowers. After the bee had warmed up, visited several flowers, and begun feeding at a normal rate, we began recording data. We timed each flower visit by speaking into a tape recorder. As soon as a flower visit was complete, we removed the flower from the arena very gently, being careful not to dislodge pollen. The details of technique followed those of Thomson (1986).

At the end of a run of about 12 flowers, we did the following to each once-visited flower. (1) We measured stigma exsertion as the distance between the tip of the longest anther and the end of the stigma after bending the stamen if necessary to lie parallel to the style (Fig. 4.3). This measure was necessarily approximate because we had to avoid any contact that might transfer or dislodge additional pollen. (2) Holding a microcentrifuge tube under the anthers to catch falling pollen, we removed the anthers with forceps, placing them in the tubes. We rinsed adhering grains off the forceps with a stream of 70% ethanol directly into the tube, thereby filling it and preserving the anthers. (3) We scored the degree of stigma-lobe recurvature on a subjective four-point scale (Fig. 4.3). (4) Again using forceps, we removed the entire stigma to a microscope slide on which had been melted a drop of fuchsin-tinted glycerin jelly. We remelted the jelly with an alcohol burner and firmly squashed the stigma under a cover slip.

The number of pollen grains that had remained in the anthers was estimated using the electronic particle counter with a 150 μ orifice. The number of pollen grains deposited on each stigma was counted using the compound microscope with ocular grid and mechanical stage.

Results

Queens of *Bombus occidentalis* are noticeably larger than those of *B. bifarius*, and they spend more time per visit (Table 4.3). For *B. occidentalis*, visit duration was related to pollen remaining at $r = -0.17$ and pollen deposited at $r = 0.32$. For *B. bifarius*, the correlations were $r = -0.22$ and $r = 0.07$ (sample sizes all >70).

Table 4.4 shows a series of general linear models by which we tried to explain variance in pollen remaining in anthers and in pollen deposited on stigmas. For analyses of pollen remaining, undehisced anther length was always included as a covariate to adjust for the number of grains the flower produced. Likewise, for analyses of pollen deposited, stigma lobe recurvature score was included as a discrete variable to adjust for the amount of receptive stigmatic surface area. These variables were not the focus of our study, but they are clearly significant and were included in the hope of increasing statistical resolution.

Our initial models were aimed at testing the effect of the bee-species × degree-of-exsertion interaction. For both pollen remaining and pollen deposited, the F statistic for this term was not significant (Table 4.4, top panel). Clearly, there was no suggestion of any interaction, and the term was dropped from subsequent models.

Stigma exsertion as a main effect showed no tendency to influence pollen remaining, but it did have a significant influence over pollen deposited (Table 4.4, middle panel). The correlation between stigma exsertion and pollen deposited after adjusting for bee species, bee individual, and stigma code was $r = -0.24$ ($N = 153$).

In the even more simplified analysis, the two *Bombus* species were found to differ in both the amount of pollen remaining and deposited (Table 4.4, bottom panel). *Bombus occidentalis* removed and deposited more pollen than *B. bifarius* (Table 4.3). Individual bees within bee species also seem to differ (although it must be admitted that bee identity was not interspersed or in any way randomized).

Discussion of Results

Plants can affect their own pollination success through influencing either visitation rates or the amount of pollen removed and deposited in a visit (Müller, 1883). Our studies of the latter revealed that strikingly little of the variance in pollen removal and deposition is explained by floral morphology and bee species. Furthermore, we found very little evidence for difference among *Bombus* species in the selection gradients they imposed on floral morphology.

Table 4.4. Analyses of variance (bottom), covariance (middle), and heterogeneity in slopes (top) for pollen remaining and pollen deposited by two Bombus *species in single visits to* Erythronium grandiflorum *flowers. Stigma exsertion is the distance between the stigma and the tip of the longest anther. Anther and stigma size are included to control for pollen production and stigmatic area, respectively. Successively simpler models are presented for each variable. In the top models, the interaction of bee species by stigma exsertion is evaluated, and found to be nonsignificant; for pollen remaining, exsertion itself is also found to be nonsignificant. In the middle model, exsertion is found to be significant for pollen deposited. The bottom models evaluate the importance of bee species ignoring morphology except for anther or stigma size.*

	Pollen Remaining in Anthers					
	df	III-SS[2]	F	df	III-SS	F
Anther or stigma size[1]	1	2790		3	11,922	
Bee species	1	2203		1	23,736	
Indiv. within bee species	13	5300		13	11,853	
Stigma exsertion	1	76	1 n.s.	1	5263	
Bee × exsertion	1	135	0.82 n.s.	1	112	0.26 n.s.
Error	137	22,533	R^2=0.35	133	56,967	R^2=0.46
Stigma size				3	11,811	9.24***
Bee species				1	26,710	29.54***
Indiv. within bee species				13	11,756	2.12*
Exsertion				1	5344	12.55**
Error				134	57,079	R^2=0.46
Anther or stigma size[1]	1	2893	17.67***	3	8361	6.03***
Bee species	1	3160	7.65*	1	27,120	34.60***
Indiv. within bee species	13	5373	2.52**	13	10,191	1.70 p=0.07
Error	139	22,764	R^2=0.35	135	62,423	R^2=0.41

[1] Anther length is a continuous covariate; stigma code is a categorical variable.

[2] Type III sums of squares for pollen remaining is ×100,000 and for pollen deposited is ×1000.

n.s. $p>0.1$:

*$p<0.05$.

**$p<0.01$.

***$p<0.001$.

For *Impatiens,* there was a suggestion that *Bombus impatiens* removed more pollen when the dimension DI was small, whereas *B. vagans* and *B. fervidus* removed more when that dimension was large. Although this is only weakly indicated, let us accept the significance of the interaction term for the sake of argument. It would exemplify our main concern—heterogeneity in selective regime that could promote adaptive divergence—but it would not fulfill Schemske and Horvitz's (1984) condition for floral specialization. The different bees would drive floral evolution in different directions even though they remove equivalent amounts of pollen. In terms of Fig. 4.1, the means are similar, but the slopes are different.

For *Erythronium,* we did find differences between bee species in the average amount of pollen moved, and pollen movement was related to stigma exsertion, but here the direction of the relationship was definitely not reversed between *Bombus occidentalis* and *B. bifarius*. Schemske and Horvitz would have found their condition met. Our interpretation is that, although there may be selection on stigma exsertion, it seems to act in the same direction regardless of bee species, an interpretation that Schemske agrees with (personal communication).

The characters we studied were, at the outset, good candidates for floral traits that might have influenced the amount of contact with pollinators' bodies, and hence the amount of pollen dispersed. It could easily be supposed that gullet-shaped flowers are molded by selection to fit their own pollinators like finely tailored gloves fit the hands for which they are made. Snapdragons (*Antirrhinum*) and turtleheads (*Chelone*) are vestibular flowers that can only be entered by large bees since they need to be pushed open. Beardstongue (*Penstemon*) species are known to differ in the size and shape of their gullet, and this difference has been attributed to adaptation to pollination by hummingbirds, wasps, and carpenter bees (Straw, 1956). Our data, however, portray jewelweed flowers as less like gloves than like mittens—one size fits all.

Among angiosperms, the spatial separation of anthers and stigma, or herkogamy as it is known, is achieved in many ways, and is generally thought to be involved in the avoidance of self-interference and self-fertilization (Webb and Lloyd, 1986; see Chapter 13). Thomson and Stratton (1985) showed that shorter-styled *Erythronium* flowers had a larger proportion of self-pollen deposited than longer-styled flowers. That stigma exsertion might (and did) have an effect on pollen deposition is not surprising. It is less clear that this character should influence the amount of pollen removed, but both the hypotheses of self-interference (Webb and Lloyd, 1986) and pollen-discounting (Holsinger and Thomson, 1994) assume a relationship between herkogamy and effective pollen removal, which we did not detect.

The interaction term pollinator species × floral morphology does not seem to have been previously of much interest to biologists working at the level of variation among individuals within a species. In order to study this, one needs to have both different species of pollinator and different floral morphologies in a factorial design. Other workers have studied how visitors differ in their effectiveness at pollination, and there have been numerous studies of how phenotypes differ in their propensity at being pollinated. A few researchers have studied both (Schemske and Horvitz, 1984, 1989; Galen et al., 1987, Galen, 1989; Stanton et al., 1991; Murcia, 1990), but the only paper we know of that presents interaction terms is that of Harder and Barrett (1993) on tristylous *Pontederia*. They found that the effect of anther level and floral-tube length on pollen removal sometimes significantly depended on bee species. In other words, there seemed to be some sporadic and weak interactions. The idea of studying how animal species and floral morphology interact to determine pollination success is better appreciated in the literature of systematics than in that of population biology, but even there it has not generally been considered as a statistical problem.

What do our two studies imply about the origin of floral diversity? Essentially, they suggest a lack of underlying heterogeneity in selection for pollination success via mechanical fit. If populations of these plants were to be broken up into a series of isolated subpopulations being visited primarily by different species of bumble bees, then there is no reason to think that they would diverge to have distinct morphologies especially suited to the different pollinators. By analogy, imagine a corral of horses. We have asked a question very similar to the following: If the gate to the corral were opened, would the horses scatter in different directions? We found no evidence that populations of plants would be driven to diverge in that way. Bear in mind, however, that we deliberately made it difficult to find interactions by choosing to compare only pollinator species within *Bombus*, and to work only with natural variation among plants at one site. Had we looked across a greater range of pollinators or a greater range of floral phenotypes, we might have detected stronger interactions.

Mechanisms of Divergence

Floral diversity is immense. Some flowers are tall and slender, others are short and fat. Some have anthers and stigmas hidden deep in the recesses of floral tubes; others present these items on open platters. Size, color, odor, and texture, as well as shape and position, vary extensively from species to species, from group to group. The range of floral architecture and ornamentation is broad, and many of the primary distinguishing features of plant taxa are floral attributes (Grant, 1949).

Flowers are to plants what male genitalia are to animals—the first among organs to diverge. Below we enumerate five ways by which divergence might arise. Probably all are important (perhaps some more than others), and they are mutually exclusive only in a particular case at a particular scale. The evolutionary scale at which morphological differences are interpreted is as important to the adaptationist's program as the spatial scale at which vegetation differences are interpreted is to the ecologist's agenda. The processes of differentiation may vary from one scale to another. For instance, in Wright's shifting balance theory, genetic drift is the initiator of divergence that moves populations off adaptive peaks, and interdemic selection is the prosecutor of further divergence toward the tops of other peaks. Consider our five mechanisms and how at different scales (and in different cases) they might vary in importance.

1. *Adaptation to distinct niches*. In contrast to later niche concepts, Elton (1927) thought of niches as existing even in the absence of organisms to fill them (see Colwell 1992). Pollinators may provide a set of discrete opportunities that plants take advantage of, in which case floral differences could represent

adaptations to different pollinators. For many dramatic contrasts, a difference in niches seems to be the best explanation. For instance, while most *Dalechampia* blossoms are pollinated by female bees that collect resin, three lineages have shifted over to being pollinated by male bees that collect fragrances (Armbruster et al., 1992; Chapter 9). In each case, the shift has been associated with interpretable character evolution, as in *D. brownsbergensis* where the resin gland has become vestigial and the stigmas have taken to secreting fruity fragrances. Likewise, it is because of a shift in pollinators that the gullet-shaped flowers of jewelweeds differ from the long-spurred flowers of garden impatiens: The former are adapted to bumble bees, the latter to butterflies. It seems problematic, however, to believe that the endless numbers of minor floral differences distinguishing species that are all pollinated by the same general type of animal are universally due to specialization on different fixed pollinator types.

2. *Character displacement.* It could be that the pollinator community offers a resource base of some particular breadth and that this resource base is partitioned, via competition, among the various plants using it. Local plant populations would then diverge as a function of local plant competitors, with the arbitrary composition of communities translating into arbitrary differences between races (and eventually species). At one time, this was a very popular mechanism to invoke, especially for characters such as flowering time (Waser, 1978; Pleasants, 1980), positioning of pollen and pollinaria on bees bodies (Dressler, 1968), and usage of specific species and castes of bees (Macior, 1982). While many examples remain plausible with some supporting evidence, they also seem far from proven. One of the best studies is that of Levin (1985) on *Phlox drummondii,* a plant that has pink flowers across most of its range and red flowers where it lives sympatrically with its pink-flowered congener *P. cuspidata.* Hybrids are more or less sterile, and thus producing hybrids rather than legitimate progeny could have been selected against. Furthermore, in experimental arrays, lepidopteran pollinators move assortatively, so that the color difference effectively decreases the proportion of hybridization events. Thus, the geographic pattern, fitness benefits, and ecological mechanisms are all consistent with an interpretation of what is known as the reinforcement of isolating barriers. Reinforcement is a special case of character displacement in which the players are close relatives selected to become different to avoid the wastage of resources associated with producing dysfunctional hybrid offspring. Although there has been interest in this mode of divergence for 40 years, there is very little evidence for or against its ubiquity (reviewed by Grant, 1994). It is not clear how often divergence occurs because flowers are selected to be different per se, as opposed to being selected to fit pollinators that happen to be different or because of less adaptive processes.

3. *Adaptive wandering.* This is the term we apply to the situation in which selection does act on characters and is responsible for character evolution, but in which the direction, strength, and manner of selection varied over time scales

that were less than those through which the characters of interest diverged. The adaptive landscape is like a bean-bag chair, always changing; selection pushes characters hither and thither, but in the end (after the selective context has shifted), it would be inaccurate to say that the various forms differ because they are adapted to different pollinators or to unique plant communities. Thus, at the scale of comparing jewelweeds to glacier lilies, it would be silly to think that the differences have resulted from adaptation to New York *Bombus* vs. Colorado *Bombus,* although during the long evolutionary history separating jewelweeds and glacier lilies, it may very well be that characters have changed due to selection in particular pollinator regimes. In contrast, it seems much more reasonable to attribute regional differences in nectar spur length in *Platanthera ciliaris* to specialization on two distinct butterfly pollinators with disparate proboscis lengths (Robertson and Wyatt, 1990). Imagine, however, that these *Platanthera* populations were to remain isolated for a very long time and were to experience a series of distinct principal pollinators. They might diverge further with each step along the way being due to selection to fit a specific pollinator, but after 10,000 or 100,000 years and perhaps dozens of faunal changes, we would not attribute their divergence to the distinctness of their pollinators at that time, and their characters might not even be especially suited to those pollinators. Adaptive wandering is driven by natural selection, not by genetic drift, so although it might appear to result in nonadaptive divergence, it would not be characterized by neutral rates of evolution, nor would the path of evolution necessarily follow a random walk. Campbell (1989) has found considerable heterogeneity in selective regime as it acts on floral dimensions among sites separated by fractions of a km and from year to year. This was in *Ipomopsis aggregata,* which is pollinated in all her sites by a few species of long-proboscised bumble bees and hummingbirds. In the shallower flowers of *Lavandula latifolia,* Herrera (1988) has documented enormous variation in pollinator assemblage (at the ordinal and species level) over a 6-year period and at several spatial scales (see Chapter 3). Since he believes that the species and orders differ in their effects on fitness and breeding system (Herrera, 1987), he concludes that this "*variation* will most likely result in shifting selection regimes." If the selection regime imposed by pollinators varies at such fine scales, what should we think about the guiding hand of selection over evolutionary time?

4. *Character correlations.* Selection may act on physiology or something else and floral characters might then be dragged along by genetic correlations without being the targets of selection themselves. Such differences would then be an epiphenomenon of selection acting through organismic complexity. Darwin (1859) repeatedly urged us not to forget "correlations of growth," which he thought are "often of the most unexpected nature" (p. 134), and he noted that differences between modules within a plant can arise through correlations just as differences arise between species, genera, and families (pp. 184–185):

> With respect to the difference in the corolla of the central and exterior flowers of a head or umbel, I do not feel at all sure that C. C. [sic] Sprengel's idea that the ray-florets serve to attract insects, whose agency is highly advantageous in the fertilization of plants of these two orders, is so far-fetched. . . . But in regard to the differences both in the internal and external structure of the seeds . . . it seems impossible that they can be in any way advantageous to the plant: yet in the Umbelliferae these differences are of such apparent importance—the seeds being in some cases, according to Tausch, orthospermous in the exterior flowers and coelospermous in the central flowers—that the elder De Candolle founded his divisions of the order on analogous differences. Hence we see that modifications of structure, viewed by systematists as of high value, may be wholly due to unknown laws of correlated growth, and without being, as far as we can see, of the slightest service to the species.

It is not at all clear to what extent floral differences have arisen through selection on correlated characters. On the one hand, it seems that genetic correlations are widespread, and that response to selection on some characters will inevitably affect others (Stebbins, 1950, p. 88). On the other hand, it seems likely that between floral traits and vegetative traits the correlations are weak, polygenic, and easily broken down if and when they are disadvantageous (Berg, 1960; Conner and Via, 1993).

5. *Genetic drift.* It is possible that many characters can vary neutrally across a broad range of states, and for those characters the random processes of meiosis and fertilization in small populations will lead to divergence. In almost any group of angiosperms, a substantial proportion of the taxonomically useful characters have no obvious selective importance, characters like whether there are few or many glands on the ovary, whether the petals are ovate or obovate, the particular shade of blue in the filaments, or the number of marginal hairs on the calyx. Why should it have ever mattered? Perhaps it didn't. Still, it should be emphasized that neutrality must be fairly extreme to allow for genetic drift in the strict sense. As Lande (1976) and many others before and since have shown, even a small amount of selection is enough to override drift in all but the smallest of populations. Wright's (1943) original example of isolation by distance was corolla color (purple vs. white) in *Linanthus parryae*. At the time, there was no reason to think that corolla color was other than neutral. Recently, however, Schemske and Bierzychudek (personal communication) have found that the color morphs do sometimes differ significantly in seed production and are thus under selection, although these differences do not seem to be due to differential pollinator attraction, so flower color itself is probably not the target of selection. This example cautions that it is very hard to say that selection on a character of interest is absent. When it is, however, drift can in theory produce substantial divergence in a relatively short period of time (Lande, 1976; Lynch, 1990). In unusually specialized systems, such as orchids and euglossine bees, Kiester et al. (1984)

have shown theoretically that drift can play an important role in coevolutionary diversification, and in tristylous systems Eckert and Barrett (1992) have presented a strong case for the importance of stochastic processes in the biased loss of some style morphs over others.

To sum up then, at a gross evolutionary scale, the contrasting characters of flowers pollinated by different types of animals are almost certainly adaptive. At the other extreme, minor distinctions may have no effect on function and would thus be neutral. As evolution proceeds, the principal governor of divergence may change. One possible progression would be drift leading to minor differences, then a niche shift leading to a striking (but not particularly multifaceted) difference, then over greater time periods the adoption of a series of environments leading to an interpretation of adaptive wandering, and finally, the fine-tuning of characters such as date-of-flowering to match the local conditions that the plants find themselves in. For diversification to be adaptive, sometime during the course of evolution, selection gradients must be heterogeneous. Our results are not consistent with the view that floral differences are initiated as adaptations to particular pollinators. These data, however, are only a first attempt at grappling with a difficult question in evolutionary biology. The pollinator-species × floral-morphology interaction term is worthy of further consideration. We do not presume that Mayr or Darwin or the Grants would have disagreed or been surprised; on the other hand, they never told us that this was how to study divergence.

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