

From:

David G. Lloyd & Spencer C. H. Barrett (Eds.), *"Floral Biology: Studies on Floral Evolution in Animal-Pollinated Plants"*. Chapman & Hall, New York, 1996.

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Floral Traits and Plant Adaptation to Insect Pollinators: A Devil's Advocate Approach

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When one considers that populations are so rich in genetic variation and that responses to artificial selection almost invariably occur, the remarkable fact is not that some populations rapidly adapt to changed conditions, but that so few do.

—D.J. Futuyma (1979)

Introduction

Certain natural history phenomena may provide a vivid illustration of selection in action and its adaptive products, and nearly every evolutionary biologist would agree that the pollination of flowers by animals provides a most illustrative example. It was surely not by chance that the first of Darwin's books to be published after *The Origin of Species* was precisely his treatise on the "contrivances by which orchids are fertilised by insects" (Darwin, 1862), the first in a series of monographs aimed at providing detailed supporting evidence for the theory of natural selection. Darwin's book on orchids evoked a major revolution in botany and gave rise to an enormous literature on pollination ecology (Ghiselin, 1984). It also marked the starting point for a tradition in the practice of pollination biology.

The Darwinian research program in pollination biology has been characterized by the search for the adaptive value of floral traits in relation to pollinating agents and, particularly, in promoting cross-pollination [see Baker (1983) for a historical account]. This activity identified a number of spectacular plant adaptations to pollinators, later becoming the textbook examples in pollination biology (including, typically, such biological oddities as fig trees, yuccas, and aroid inflorescences). However, the success of this research program was not restricted to identification of such canonical examples in pollination biology, as most interactions between plants and pollinators certainly are much less spectacular. The elucidation of relationships between the major pollinators of a plant species and particular combinations of structural and functional floral features ("pollination syndromes") was a further important achievement. The convergence of the flow-

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ers of disparate plant lineages into relatively few distinct floral types, along with their rather predictable association with pollination by different higher taxa of animals, was taken as *prima facie* evidence of adaptation by plants to their animal pollinators (Baker, 1961; Percival, 1965; Faegri and van der Pijl, 1966; Baker and Hurd, 1968; Proctor and Yeo, 1973). Most progress in pollination biology resulted from interspecific comparisons, and it has only been in the last two decades that pollination studies included intraspecific analyses, involving natural or experimentally induced variation in floral traits (e.g., Waser, 1983a; Nilsson, 1988; Galen, 1989; C.M. Herrera, 1993; and references therein). This latter approach led to analyses of the reproductive consequences of intraspecific variation in the arrangement, color, scent, morphometry, and shape of animal-pollinated flowers. By adopting a "phenotypic selection" approach (Lande and Arnold, 1983; Arnold and Wade, 1984), some of these investigations quantified pollinator-mediated selection on floral traits (e.g., Galen and Newport, 1988; Nilsson, 1988; Campbell, 1989; Galen, 1989; Schemske and Horvitz 1989; Robertson and Wyatt, 1990; C.M. Herrera, 1993; Anderson and Widén, 1993).

The century-old, Darwinian approach to pollination biology has thus established two important *qualitative* conclusions, namely that certain floral traits of some animal-pollinated plants must be interpreted as adaptations to pollinating agents, and that animal pollinators can effectively exert selective pressures on floral traits. The array of proximate mechanisms by which pollinators exert their selective pressures on plants is also reasonably well understood. In contrast, we are still profoundly ignorant of some *quantitative* aspects that are equally relevant from an evolutionary perspective. Demonstration that pollinators exert selection on some floral traits and that plants can respond to such selection does not verify either that both phenomena occur universally or that most or all floral traits of every insect-pollinated plant have been shaped in evolutionary time by the selective action of their current pollinating agents. (Reciprocally, demonstration that adaptations of plants to their pollinators are not universal in nature would not detract from the validity of any well-documented case of floral adaptation.) Two questions immediately arise if one accepts this conceptual distinction between the certainty that a phenomenon occurs and its actual frequency of occurrence. First, how common are species whose floral traits were predominantly shaped by selection from their pollinators (i.e., have evolved in response to the latter's selective pressures)? Second, how much of the floral phenotype of an average animal-pollinated plant has arisen as a consequence of selection exerted by pollinators? These two questions are subsumed by the less formal question, how widespread are floral adaptations to pollinators in nature?

Rather than attempting to answer these questions conclusively, the main aim of this contribution is to call attention to the actual relevance, and potential implications, of the questions themselves. Although foreign to mainstream tradition in pollination biology, the issue of the relative frequency of floral adaptations to pollinators deserves more consideration than it has received so far [but see

Schemske (1983), Waser (1983a), Howe (1984)]. I will first briefly review selected evidence that justifies questioning the commonness of floral adaptation to pollinators. Then, I quantitatively analyze the patterns of intraspecific variation in corolla-tube depth of insect-pollinated plants in a region of southeastern Spain, to illustrate that the above questions are amenable to rigorous quantitative testing. Finally, I enumerate some ecological factors that may constrain either the strength of selection by pollinators on plants, or the latter's response to such selection.

Despite its central role in evolutionary biology, there are numerous, often conflicting, definitions of the concept of "adaptation," and no consensus seems yet to exist about the requisites needed to identify a given phenotypic trait as an adaptation (e.g., Williams, 1966; Endler, 1986; Reeve and Sherman, 1993). In some cases, my reasoning will be based on the distinction between "exaptation" and *sensu stricto* adaptation suggested by Gould and Vrba (1982), a "history-laden" definition of adaptation (Reeve and Sherman, 1993). Under this view, true floral adaptations to pollinators would involve features that promote fitness *and* were built by selection exerted by current pollinators. In contrast, floral exaptations are characters that, although contributing to fitness, did not evolve as a consequence of selection by current pollinators. In other cases, I will adhere to a nonhistorical definition of adaptation. Under this view, which underlies all studies adopting the phenotypic selection approach, an adaptation is a phenotypic variant that enjoys the highest fitness among a specified set of variants in a given environment, irrespective of its history. This inconsistency of usages is chosen deliberately to examine whether questions about the frequency of occurrence of floral adaptations to pollinators are definition-dependent or, on the contrary, make sense regardless of the particular definition of adaptation one adheres to.

Some Cautionary Tales

Questions about the frequency of occurrence of floral adaptation to pollinators make sense only given the assumption that floral traits do not always represent adaptations to a plant's pollinators. I am not aware of any radical claim that all floral traits of all species exemplify actual adaptations, and every pollination biologist would certainly deny such imputation. Nevertheless, and probably for reasons less related to biology than to a well-defined tradition that had its inception in the urgent need to gather support for the newly born evolutionary theory, positive evidence for floral adaptations has traditionally been sought, publicized, and given more weight than possible negative evidence. However, independent lines of evidence caution us that a plant's floral traits need not represent adaptations to its pollinators.

Pollinator Diversity

Indiscriminate application of the concept of pollination syndromes has tended to exaggerate artificially the degree of adaptation of plants to pollinators (Baker,

1963; Macior, 1971; Waser, 1983b). In practice, the floral traits that characterize syndromes (e.g., color, shape, symmetry, nectar production) are generally of little use in predicting the pollinators of a given plant species. Furthermore, there is now overwhelming evidence that syndromes are of little value in explaining interspecific variation in pollinator composition (e.g., J. Herrera, 1988; Olesen, 1988; McCall and Primack, 1992; Waser and Price, 1990). I further illustrate this lack of conformity between syndromes and pollinator composition by examining the actual pollinator diversity experienced by insect-pollinated plants in nature.

The diversity of insects pollinating a given plant species can be evaluated at different levels in the taxonomic hierarchy, but the diversity of insect orders is particularly informative, as these higher-level taxa have been generally associated with different suites of floral characters or syndromes. I compiled information on the number of insect orders visiting the flowers of individual plant species in seven habitats on different continents. I selected studies providing comprehensive information on the flower visitors of at least 20 locally or regionally coexisting plant species. In one case (site 1 in Fig. 3.1), no reliable information is available to assess the extent to which flower visitors were pollinators. In four cases (sites 2–4 and 7 in Fig. 3.1), information presented by the authors indicates that most or all taxa involved were pollinators. In the remaining two cases (sites 5 and 6 in Fig. 3.1), there was evidence that all flower visitors were pollinators. As

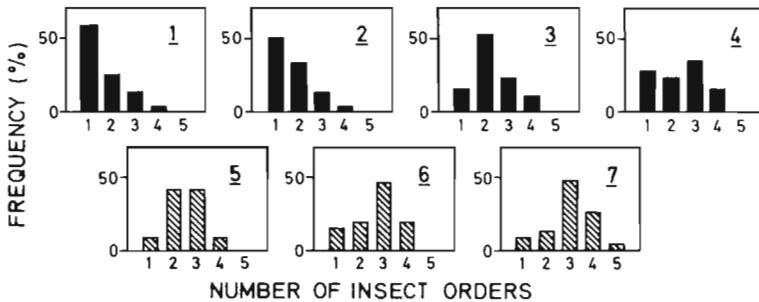


Figure 3.1. Ordinal diversity of insect floral visitors to plants in three Mediterranean (lower row, hatched bars) and four non-Mediterranean (upper row, filled bars) habitats. Each graph depicts the frequency distribution of the number of insect orders visiting the flowers of individual plant species in each habitat, coded as follows: 1, coastal tropical scrub, Jamaica (Percival, 1974) ($N = 60$ plant species); 2, montane temperate scrub, Chilean Andes (Kalin Arroyo et al., 1982) ($N = 121$ species); 3, alpine and montane habitats, Australia (Inouye and Pyke, 1988) ($N = 40$ species); 4, subalpine grassland and scrub, New Zealand (Primack, 1983) ($N = 108$ species); 5, montane scrub and woodlands, Sierra de Cazorla, southeastern Spain (Jordano, 1990; C. M. Herrera, unpublished) ($N = 34$ species); 6, coastal scrub, Doñana National Park, southwestern Spain (J. Herrera, 1985, 1988) ($N = 26$ species); 7, coastal scrub in Barcelona, northeastern Spain (Bosch, 1986, 1992; Retana et al., unpublished) ($N = 23$ species).

would be expected, insect orders were the same in all plant communities, namely, Hymenoptera, Coleoptera, Diptera, and Lepidoptera (a fifth order, Heteroptera, was recorded at a single site). Although sites differed somewhat in the frequency distributions of the number of insect orders visiting individual plant species, the prevailing picture from these studies is that, in most sites, a large fraction of plant species are pollinated by two or more insect orders (Fig. 3.1). This was particularly marked at the three Mediterranean sites, where plant species were pollinated by an average of 2.7 insect orders (the three sites combined).

Each of the major insect orders involved in the above pollination studies is generally associated with a distinct suite of floral characters or pollination syndrome (Percival, 1965; Faegri and van der Pijl, 1966; Baker and Hurd, 1968). Presumably each syndrome exemplifies alternative adaptive pathways to differences among higher insect taxa in sensory abilities, nutritional requirements, mobility, and morphology. The relatively loose association of plants to particular insect orders for pollination may indicate a prevailing low degree of floral specialization to particular pollinators. Alternatively, the result might reflect some bias in the composition of the species considered with regard to floral morphology. For instance, this could occur if the species involved primarily produced "unspecialized" flowers with exposed floral rewards and an absence of structural or functional features that restrict the morphological or behavioral range of insect visitors. However, there is no evidence that this was the case with the species sampled. In the three Mediterranean sites, precisely where plants had the highest taxonomic diversity of pollinators, species with tubular corollas and concealed floral rewards accounted for between 50–76% of species in each site. Furthermore, in none of the three Mediterranean sites were species with exposed floral rewards (dish-shaped corollas) visited by more insect orders than those with concealed rewards (tubular corollas) (Table 3.1). McCall and Primack (1992), in an investigation of the pollination biology of three widely contrasting habitats, also found that the insect orders visiting flowers with open and tubular corollas were essentially identical.

Table 3.1 Mean (± 1 SD) number of insect orders visiting the flowers of species with open and tubular corollas at three Spanish sites (sites 5–7 in Fig. 3.1). Number of plant species in each category (sample size for means) in parentheses. Difference between floral types tested with single-factor ANOVAs (data square root-transformed for the analysis).

Site	Flower Type		Significance of Difference (<i>P</i> -value)
	Tubular	Open	
Cazorla	2.5 \pm 0.7 (25)	2.6 \pm 1.1 (8)	0.90
Doñana	2.7 \pm 1.0 (13)	2.7 \pm 1.0 (13)	0.98
Barcelona	3.0 \pm 1.1 (15)	3.1 \pm 0.7 (7)	0.81

Successful Pollination and Adaptation

The observation that the floral morphology and function of a given plant “fit nicely” the energetic, morphological, or behavioral traits of their pollinators has frequently prompted adaptive interpretations. However, that kind of evidence may convey little information about the origin of floral adaptations, because plants may be quite successfully pollinated even though the floral traits at work did not actually evolve in relation to their present pollinators. In other words, floral traits are often exaptations rather than *sensu stricto* adaptations.

Large-scale “experiments” brought about by human-induced, artificial expansions of plant geographical ranges provide unequivocal support for this claim. In contrast with the oft-quoted, popular examples of alfalfa and red clover (Faegri and van der Pijl, 1966; Proctor and Yeo, 1973), plants introduced into foreign continents for ornamental or commercial purposes provide many examples of successful pollination by completely new pollinator assemblages (e.g., Rick, 1950; Milton and Moll, 1982; Smith, 1988; Podoler et al., 1984; Kohn and Barrett, 1992). The phenomenon is quite familiar to keepers of botanical gardens, where artificial assortments of exotic plants are often successfully pollinated by pollinator assemblages whose taxonomic composition differs dramatically from those found by the plants in their native habitats. Heterostyly is a pollination mechanism where close reciprocal correspondence between the flower and particular pollinators seems most critical for successful pollination (Darwin, 1877; Ganders, 1979). Yet Kohn and Barrett (1992) found that the polymorphism in *Eichhornia paniculata* functioned in a similar manner in its native Northeastern Brazil and Canada, where it is an introduced plant and pollinated by bumble bees (which do not visit the plant in its native region).

When introduced plants are involved, we are aware that there is no history of interaction between the plants and their newly acquired pollinators (a prerequisite for the existence of adaptations if one adheres to a history-laden definition of the term), and no one would dare to propose adaptive explanations in these cases. But the success of pollination systems in the absence of a shared history of interactions between plants and pollinators is not restricted to cases affected by human intervention, and it may also occur in much less evident contexts. At least 12 species and six genera of typical “bird-flowers” (red-orange-yellow large corollas, plenty of nectar, little or no scent) occur on the Canary Islands and Madeira, yet no true flower-birds occur in these islands. That set of plants is successfully pollinated by several species of sylviid warblers that feed opportunistically on nectar (Vogel et al., 1984; Olesen, 1985). Although the plants involved are endemic relicts surviving from tertiary tropical or subtropical forests, their current avian pollinators are widely distributed in the western Palaearctic region and have originated more recently. The most likely interpretation in this case is that the modern avian visitors of Canarian bird flowers are newcomers to the scenario, and are not the original pollinators that interacted with these plants in

the continental tertiary flora where they originated (Vogel et al., 1984; Olesen, 1985). Pollination of these plants is thus successfully accomplished by pollinators they certainly are not adapted to.

I close this section by describing an example from my own investigation (C.M. Herrera, 1993) that further documents the perils of inferring adaptation to present pollinators from simple observations of morphological matching. A nonhistorical definition of adaptation is adopted on this occasion. *Viola cazorlensis* is an endemic violet from southeastern Spain whose reproductive peculiarities make it a particularly favorable subject for investigating the adaptedness of floral morphology. The species is characterized by a closed corolla with a long, thin spur (mean = 25.0 mm, range = 8–42 mm), the longest of all European species in its genus. *Viola cazorlensis* also has the longest corolla tube of all regionally coexisting species with tubular corollas in its native range (see below). The shape of the corolla and size of flower parts (including spur length) vary widely among individuals. Nectar accumulates at the tip of the spur and, due to the highly restrictive floral morphology, pollination is accomplished by virtually a single species of day-flying hawkmoth (*Macroglossum stellatarum*), an unusual feature for the genus *Viola* (Beattie, 1974). Hawkmoth pollination systems generally involve sets of Sphingidae rather than single species, and documented cases of monophily are rare (Nilsson et al., 1985, 1987). Mean spur length of *V. cazorlensis* flowers matches nearly perfectly the mean proboscis length of *M. stellatarum* (26.4 mm). These observations might suggest that the unusually long (relative to congeneric species) spur of *V. cazorlensis* evolved in response to directional selection from its sole long-tongued pollinator. This hypothesis would be supported if spur length were significantly related to maternal fecundity, as found in other species with long tubular corollas (Nilsson, 1988). I tested this prediction in a 4-year study of seed production and, although flower size (peduncle length, size of petals) and shape (corolla outline) experienced significant phenotypic selection, spur length did not. In fact, the latter characteristic was precisely the only floral trait among those examined yielding negative evidence of phenotypic selection. Results thus did not support an interpretation of the characteristic long spur of *V. cazorlensis* as an adaptation to its current pollinator.

Pollinator Selection and Variability in Corolla-Tube Depth

Corolla-tube length has perhaps evoked adaptive interpretations more often than any other floral trait. Indeed, correlations have been found between the distributions of corolla-tube length and the length distribution of pollinators' mouthparts across regional floras (Inouye, 1979; Inouye and Pyke, 1988). For this reason, corolla-tube length seemed an appropriate character to quantitatively test the adaptedness of floral phenotypes to pollinators. The unanticipated results for *V. cazorlensis* mentioned above encouraged me to study patterns of corolla-tube length in a diverse regional species assemblage that included this species.

Hypotheses and Predictions

Darwin (1862) envisaged the evolution of flowers with deep corolla tubes as an "evolutionary race" between plants and pollinating agents resulting in directional selection for increased corolla length. Nilsson (1988) found evidence of directional phenotypic selection on corolla depth in two temperate orchids but, as noted earlier, I failed to find it for *V. cazorlensis*. This disagreement suggests that not all flowers with deep corolla tubes exemplify adaptation to current pollinators.

Fenster (1991) provided a quantitative tool for testing the generality of floral adaptedness to pollinators in plant species assemblages. Fenster's hypothesis relies on two demonstrable assumptions. First, increasing corolla-tube length is accompanied by reduced taxonomic diversity of pollinators and increased specificity of pollen placement on pollinators' bodies (Fenster, 1991). Second, pollinator taxa ordinarily differ in important components of pollinating effectiveness, and thus in the nature of their potential selective pressures on plants (e.g., Price and Waser, 1979; Motten et al., 1981; Schemske and Horvitz, 1984; C.M. Herrera 1987a). Given these relations, the strength of selection (either stabilizing or directional) on corolla-tube length will increase with increasing corolla-tube length. Based on these considerations, and the demonstration that *both* stabilizing and directional selection decrease the phenotypic variance of characters subject to selection (Lande and Arnold, 1983), Fenster predicted that, under selection by pollinators, the phenotypic variance of corolla depth should be negatively correlated with mean corolla depth. He found support for the prediction among 10 hummingbird-pollinated species.

I now test this hypothesis for a larger set of insect-pollinated plants from southeastern Spain. The following questions will be addressed: (1) Do most or all species exhibit significant individual variation in corolla depth? (2) Do species differ in the extent of individual variability in corolla depth? And if they do, (3) does variability vary inversely (across species) with mean depth? Questions 1 and 2, although not originally associated with Fenster's prediction (question 3), are directly relevant to the proper interpretation of results.

Methods

I measured corolla-tube depth for 58 insect-pollinated species from the Sierra de Cazorla region in southeastern Spain. Species were selected for study on the basis of the morphology of their corollas, and were sampled from a number of habitat types, including scrublands, mixed montane woodlands, forest edges, and disturbed places. I chose species with tubular corollas with fused petals, closed corollas with spurred petals, or functionally tubular corollas formed by fusion of sepals even though the petals themselves were not fused. Whenever possible, I measured at least 100 flowers for each species (5 flowers from each

of 20 randomly chosen plants from a single locality; see the appendix to this chapter for species and sample sizes). Detailed data on the composition of pollinator faunas are available for only approximately 25% of species in the sample. Although limited, these data indicate that the assumption of Fenster's hypothesis of decreasing pollinator diversity with increasing corolla depth holds for my sample. In particular, species with corolla tubes >20 mm (near the upper extreme of the range for all species) are each pollinated by 1–11 insect species, whereas those with corolla depths <10 mm are pollinated by up to 90 insect taxa (J. Herrera, 1985; C.M. Herrera, 1988, 1993, and unpublished; Jordano, 1990).

To obtain comparable measurements (from a pollinator's perspective) of tube length from flowers of different morphologies, I used a measuring device that simulated an insect proboscis. This device consisted of a piece of fine (0.25-mm diameter), flexible nylon thread fitted inside a tubular plastic sheathing (1.5-mm diameter). The nylon thread was gently pushed into the corolla aperture, mimicking an insect pollinator probing the flower's interior for nectar. When the nylon thread could not be inserted further, I slid the plastic sheathing down the thread until it was impeded by some floral structure (generally the anthers or some perianth part). Sheath and thread were then held together, drawn from the flower, and the straightened length of thread protruding from the edge of the sheath was measured to the nearest 0.05 mm with a digital caliper. The nylon thread behaved much like a moderately rigid bumble bee or bee-fly proboscis when inserted into short, straight corollas, and it also served as an acceptable analogue of a hawkmoth or butterfly proboscis when applied to long, curved corollas or spurs. I am confident that this method produced truly comparable measurements of effective corolla depth.

Results

Mean corolla depth was computed separately for each plant and these "individual means" were then averaged to obtain species means (listed in the appendix). Species means ranged between 4.2–29.6 mm (Fig. 3.2A). Most species exhibited moderate individual variation in corolla depth, with coefficients of variation (CV) generally falling in the range 10–25% (Fig. 3.2B). Three of the five species with CV's >30% were gynodioecious. In these species, perfect-flowered individuals had significantly deeper corollas than male-sterile ones, and this dimorphism was responsible for the increased intraspecific variability. Individual variation in mean corolla depth was highly significant in all except one species (see the appendix), and the proportion of intraspecific variance accounted for by individual variation ranged between 13–94% (Fig. 3.2C).

I tested the significance of interspecific differences in variability with the variant of Levene's method proposed by Sokal and Braumann (1980). Individual means (Y_{ij}) were first log-transformed, and then the absolute deviates with respect

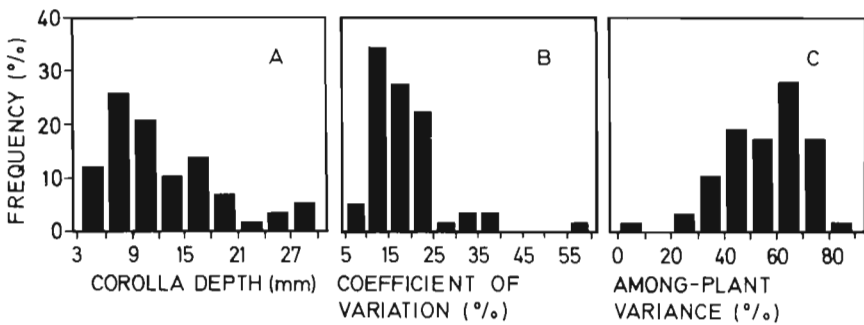


Figure 3.2. Summary of intra- and interspecific variation in corolla depth for 58 insect-pollinated species with tubular corollas from the Sierra de Cazorla region in southeastern Spain (see the appendix). Shown are frequency distributions of (A) species means, (B) coefficients of variation, and (C) proportion of total intraspecific variance accounted for by individual variation (“among-plant variance”).

to the species mean of these transformed values were computed as $d_{ij} = |\log Y_{ij} - \log \bar{Y}_i|$, where d_{ij} and Y_{ij} are, respectively, the deviate and mean corolla depth of the j th individual in the i th species, and $\log \bar{Y}_i$ is the mean of the logarithms of the i th species. Absolute deviates d_{ij} were then compared across species using Kruskal–Wallis nonparametric analysis of variance (excluding gynodioecious species, which would have artificially inflated interspecific heterogeneity). Species differed significantly in individual variability of corolla depth ($\chi^2 = 136.5$, $df = 54$, $P \ll 0.001$).

The variance of log-transformed individual means [$\text{var}(\log Y_{ij})$] was computed for each species, and the resulting figures plotted against species means (Fig. 3.3). Variance and mean were uncorrelated, regardless of whether the three gynodioecious species were included ($r_s = -0.070$) or not ($r_s = 0.045$) in the computations. Nonparametric regression analyses similarly failed to reveal any relationship between variance and mean of corolla depth (Fig. 3.3).

As species are related among themselves to varying degrees and belong to a common phylogeny, the data in Fig. 3.3 do not represent statistically independent observations. To account for the influence of possible phylogenetic correlations (Felsenstein, 1985; Harvey and Pagel, 1991; Gittleman and Luh, 1992), I applied a modification of the pairwise comparative method proposed by Møller and Birkhead (1992) (see also Lessios, 1990) to the 27 species belonging to genera represented by at least two species. All possible species pairs were constructed within each genus, and the relationship between variance and mean corolla depth was scored in each case as positive (increased variance with increased mean) or negative (decreased variance with increased mean). Of the 27 pairwise, intragenetic contrasts, 17 scored negative, and thus in the direction predicted by Fenster’s hypothesis. The probability of obtaining by chance alone as many negative scores is 0.124 (from the binomial distribution); hence, the hypothesis of a negative

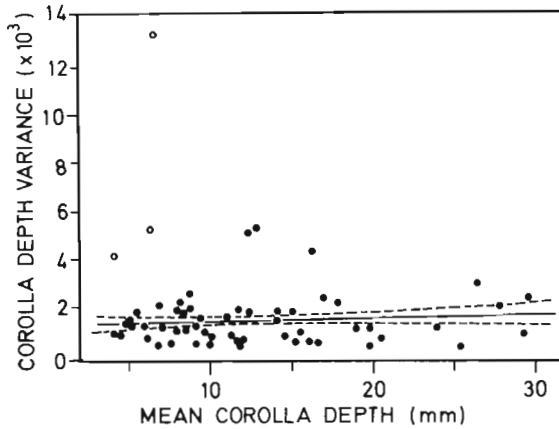


Figure 3.3. Relation of individual variance (variance of log-transformed individual means) to mean corolla depth for 58 southeastern Spanish species (see the appendix). Gynodioecious species (characterized by floral dimorphism and hence high variance in corolla depth) are shown as open dots. The illustrated regression line (continuous line) for all species, except the gynodioecious species, was fitted using a nonparametric procedure (cubic splines obtained by the generalized cross-validation method; Schluter, 1988). Dotted lines indicate ± 1 SE of mean predicted values from 1000 bootstrap regression replicates.

relationship between variance and mean is not supported when the statistical nonindependence of data points is controlled by restricting the analysis to pairs of closely related, congeneric species. It may therefore be concluded that, in the set of species studied, no significant relationship exists between variability and mean corolla-tube depth. This result is not consistent with the idea of generalized selection by pollinators on this floral trait in the study region, and confirms in a broad species assemblage the findings obtained for *Viola cazorlensis*.

Ecological Constraints on Floral Adaptation

The degree of adaptedness of plants to pollinators may be limited by factors intrinsic or extrinsic to the plants. Well-known intrinsic limitations include, for instance, genetic factors and life history or developmental constraints (Futuyma, 1979; Howe, 1984; Kochmer and Handel, 1986; Zimmerman et al., 1989), and I will not consider them here. This section will focus on extrinsic, or ecological, factors. For convenience, these can be classed into two nonexclusive categories depending on whether they reduce the probability of occurrence of selection by pollinators, or limit responses to selection when this effectively occurs. The two sections below examine some of these factors.

Constraints on the Occurrence of Selection

Spatio-temporal unpredictability in the composition of pollinator assemblages is probably one of the most important factors reducing the possibilities of selection on floral traits by pollinators. Whenever comparative studies have been undertaken, the pollinators of a given plant species have been shown to vary in their effects on plant reproductive success, an important fitness component. This variation may be due to differences in the frequency or amount of pollen removal or delivery, "quality" of delivered pollen from the viewpoint of the recipient plant, or some combination of these (e.g., Price and Waser, 1979; Motten et al., 1981; Schemske and Horvitz, 1984; C.M. Herrera, 1987a; Davis, 1987; Snow and Roubik, 1987; Ramsey, 1988; Wolfe and Barrett, 1989; Wilson and Thomson, 1991; Harder and Barrett, 1993). This variation provides, in theory, the opportunity for plants to specialize on (meaning to become adapted to) taxa providing the best pollinator services. Nevertheless, variation at various temporal and spatial scales in the composition and relative abundance of pollinators will most often limit seriously this possibility. Recent studies have shown that plants generally experience complex spatio-temporal mosaics in their pollinator assemblages, whose composition and abundance often vary tremendously between years and locations (C.M. Herrera, 1988; Waser and Price, 1990; Pettersson, 1991; Eckhart, 1992). Differences between plant populations in pollinator abundance and composition reflect the patterning in space of animal populations, whereas seasonal or annual variations reflect the population fluctuations of component species. For insects, annual fluctuations are universal even in the "stable" tropics (Wolda, 1983), and even affect the epitome of specialized pollinators, euglossine bees (Horvitz and Schemske, 1990). The stochastic nature of much of this spatio-temporal variation in pollinator composition, coupled with differences between pollinator taxa in pollinating effectiveness, will result in an inconstant pollination regime, as illustrated in Fig. 3.4 for a population of the insect-pollinated *Lavandula latifolia* in southeastern Spain. This species is pollinated by hymenopterans, lepidopterans, and, to lesser degree, dipterans. Compared to lepidopterans, hymenopterans transfer pollen to stigmas more often, and fly shorter distances between consecutive flower visits (thus promoting more geitonogamy) (C.M. Herrera, 1987a). The relative proportions of these major groups of pollinators vary annually, thus inducing fluctuations in average probability of pollen transfer per pollinator visit and mean flight distance between consecutive visits (Fig. 3.4). The variation in time and space of these and other important variables in the pollination environment generates a heterogeneous selective regime for plants, which weakens selection on floral traits (Schemske and Horvitz, 1989; C.M. Herrera, 1988; Horvitz and Schemske, 1990; Eckhart, 1991). For instance, in the bee-pollinated *Calathea ovandensis*, Schemske and Horvitz (1989) detected phenotypic selection on corolla-tube length during only one of three reproductive episodes because of marked annual variation in the composition of the pollinator fauna.

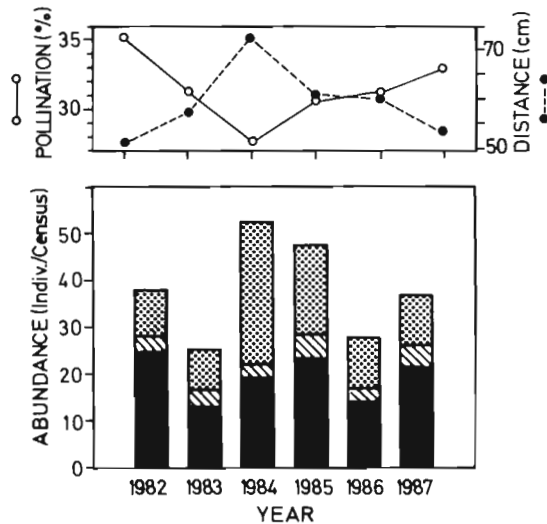


Figure 3.4. Annual variation in the composition of the insect pollinator assemblage of *Lavandula latifolia* at the Sierra de Cazorla, southeastern Spain (lower graph; solid, dashed, and dotted portions of bars correspond to hymenopterans, dipterans, and lepidopterans, respectively), and concomitant changes in the predicted mean distance flown by pollinators between consecutive floral visits ("distance") and the proportion of floral visits resulting in pollen delivery to the stigma ("% pollination"; upper graph). Data in the upper graph are averages weighted by the abundance of the different pollinators. Based on data in C. M. Herrera (1987a, b, 1988).

Expectations of floral adaptedness rely, to a considerable degree, on acceptance of Stebbins' (1970) "most effective pollinator principle," which states that "the characteristics of the flower will be molded by those pollinators that visit it most frequently *and* effectively in the region where it is evolving" (*italics added*). Nevertheless, pollinators providing pollination of higher quality are generally neither the most abundant nor the most predictable in time or space, thereby limiting the possibilities of selection on floral traits. For instance, although both diurnal and nocturnal visitors pollinate *Asclepias syriaca*, the latter provide higher-quality pollination (more pods produced per pollinator visit), but diurnal flower visitors are more abundant and eventually account for most effective pollinations (Bertin and Willson, 1980; Jennersten and Morse, 1991). An analogous situation was reported by Guitián et al. (1993) for the bee- (diurnal) and hawkmoth- (nocturnal) pollinated *Lonicera etrusca*. There have been relatively few investigations simultaneously studying pollinator effectiveness and abundance, but they suggest that decoupling of abundance and pollinating quality occurs frequently among insect-pollinated plants (Montalvo and Ackerman, 1986; Sugden, 1986; Schemske and Horvitz, 1989; Pettersson, 1991). *Lavandula latifolia* provides a further example. In a southeastern Spanish locality, pollinators of this species differ in several aspects of pollinating effectiveness, including

the proportion of floral visits that result in effective pollen deposition to the stigma (C.M. Herrera, 1987a). They also differ broadly in mean abundance and extent of annual variation in abundance (C.M. Herrera, 1988). In this set of pollinators, pollinating effectiveness (measured as the proportion of visits resulting in effective pollen transfer) was unrelated to either mean abundance or population variability over a 6-year period (Fig. 3.5).

Constraints on the Response to Selection

Ecological factors may constrain adaptive responses of plants to selection by pollinators even when selection actually occurs. Recent studies have demonstrated phenotypic selection on floral traits (see references in the introduction); however, few of these studies evaluated the importance of variation in floral traits relative to other concurrent factors that can also influence fitness in natural populations. Even if variation in a given floral trait correlates significantly with differential reproductive success, the proportion of within-population variance in reproductive success explained by that attribute may vary widely, depending on the relative importance of other factors (Schemske and Horvitz, 1988; C.M. Herrera, 1993). Studies of phenotypic selection on floral traits have often shown that a statistically significant proportion of the “opportunity for selection” (the variance in fitness) depends on the existence of individual variation in floral traits, but the magnitude of this proportion has rarely been evaluated. In the *Calathea*

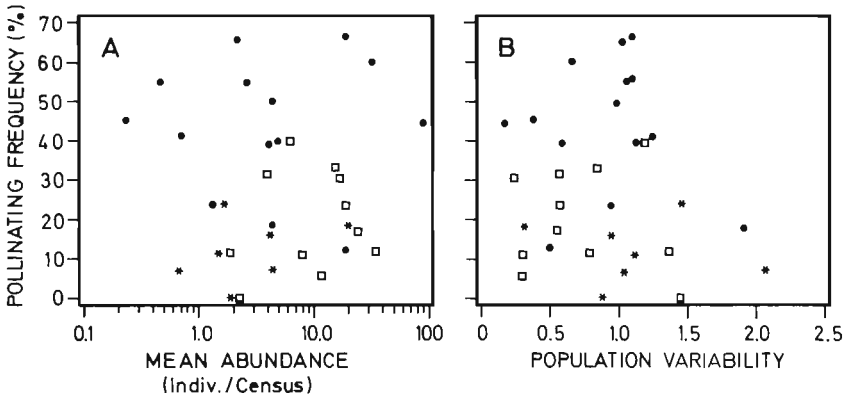


Figure 3.5. Relation between the frequency of pollen deposition on stigmas per visit (“pollinating frequency”) and (A) mean abundance and (B) population variability of insect pollinators in a *Lavandula latifolia* population over a 6-year period ($N = 32$ insect taxa; hymenopterans, lepidopterans, and dipterans are coded, respectively, by dots, squares, and stars). Population variability is measured by the standard deviation of the natural logarithm of species abundance (Williamson, 1972). Pollinator effectiveness is unrelated to either abundance ($r_s = 0.060$, $P = 0.74$) or population variability ($r_s = -0.006$, $P = 0.97$) in this pollinator assemblage. Based on data in C. M. Herrera (1987a, 1988).

ovandensis study mentioned above, individual variation in corolla depth accounted for only 8% of total variance in fruit production in the single year when selection occurred (Schemske and Horvitz, 1988, 1989). In *Viola cazortensis*, individual variation in floral morphology (corolla shape and petal and peduncle length) explained only 2% of total variation in fruit production (C.M. Herrera, 1993). Despite the statistical significance of selection on components of floral morphology, other factors (e.g., herbivory, microhabitat type, size differences) caused considerable variation in fecundity in these species, so that phenotypic selection on floral morphology probably has little impact on individual variation in maternal fitness. The opportunity for selection in these species was therefore only minimally attributable to phenotypic variance in floral morphology. More field studies on natural populations are needed to evaluate the generality of these results, but they suggest that selection on floral traits, even when it occurs, may be heavily "diluted" by the overwhelming influence of other factors (Schemske and Horvitz, 1988; C.M. Herrera, 1993). Maternal fecundity is only one possible component of fitness in hermaphroditic plants and it may be argued that selection on floral morphology via the male function might still occur in the cases mentioned above (Primack and Kang, 1989). However, studies on natural populations of hermaphroditic plants have documented close correlations (across individuals) between absolute measures of reproductive success via pollen (seeds sired) and ovules (seeds produced) (Broyles and Wyatt, 1990; Devlin and Ellstrand, 1990; Dudash, 1991), thus suggesting that maternal fecundity figures often represent satisfactory estimates of fitness.

Concluding Remarks

I have shown in the preceding sections that independent lines of evidence justify questions about the actual frequency of occurrence of floral adaptations to pollinators in nature. First, patterns of phenotypic variation in corolla depth in a regional species assemblage are not consistent with the idea of generalized selection by pollinators on this floral trait. Second, apart from possible intrinsic factors limiting adaptedness of plants to pollinators (e.g., life history or genetic constraints), ecological mechanisms often limit both the occurrence of pollinator selection on plants and the likelihood of adaptive responses. At the very least, these observations highlight the need to expand the prevailing tradition in pollination biology to include in its research program the additional set of questions outlined in the introduction.

Disagreements with the main tenet of this contribution will likely stem from discrepancies with my usage of the concept of "adaptation." As stressed in the introduction, there is not a common agreement about its meaning, and definitions may be classed into either "history-laden" or nonhistorical categories (Reeve and Sherman, 1993). I have indistinctly adhered to the two definitions, and this inconsistency has proven useful to illustrate that questions about the frequency

of occurrence of floral adaptations to pollinators make sense, regardless of the particular definition of adaptation one adheres to.

We already understand how and why floral adaptations may come about, but we still need to know how frequent their occurrence is in nature. Plant interactions with animals for reproduction may successfully persist even in the absence of mutual adaptation and a shared history of interaction between counterparts. Consequently, animal-related plant traits, including floral ones, may persist unchanged for extended geological periods (C.M. Herrera, 1986, 1992). Some floral traits probably are exaptations rather than actual adaptations to present-day pollinators, whereas others may even be inconsequential in terms of differential fitness. Evolutionary pollination biologists should not let "the appeal of orderly pollination syndromes" (Waser and Price, 1990) obscure the richness and complexities involved in the relationship between plants and their floral visitors, and include in their research program an unprejudiced, unbiased scrutiny of the relative frequencies of occurrence of floral adaptations and exaptations in nature. After more than a century of successfully following Darwin's lead in search of support for evolutionary theory, there is no longer any question about the real occurrence of plant adaptations to pollinators: The time is now ripe to ask about their universality. Evolutionary theory would certainly not be challenged in any serious way by accepting that such adaptations may not occur. The question is, how often?

Appendix

Summary of corolla depth measurements for 58 insect-pollinated plants with tubular corollas from the Sierra de Cazorla region, southeastern Spain. Shown are the number of flowers (N_f) and individuals (N_i) sampled for each species, and the mean, standard deviation (SD), and coefficient of variation (CV) of individual means. Significance of individual variation was tested using single factor ANOVAs (P -values < 0.001 are shown using exponential notation).

Species	N_f	N_i	Mean (mm)	SD	CV (%)	Individual Variation	
						F -value	P
<i>Acinos alpinus</i>	100	20	11.94	1.58	13.3	7.76	2E-11
<i>Anarrhinum bellidifolium</i>	100	20	4.17	0.65	15.5	7.85	1E-11
<i>Anchusa azurea</i>	93	20	11.79	2.60	22.0	18.71	8E-21
<i>Anchusa undulata</i>	98	20	11.09	1.96	17.7	14.91	1E-18
<i>Ballota hirsuta</i>	100	20	9.19	1.64	17.8	33.79	2E-30
<i>Calamintha sylvatica</i>	100	20	11.41	1.62	14.3	12.70	6E-17
<i>Cerinth major</i>	93	21	19.82	1.74	8.8	19.41	2E-21
<i>Chaenorhinum serpyllifolium</i>	90	20	16.14	1.73	10.7	5.64	41E-9
<i>Cleonia lusitanica</i>	79	25	16.33	3.61	22.1	5.90	33E-9
<i>Coris monspeliensis</i>	89	19	5.53	1.10	20.0	7.42	3E-10
<i>Dactylorhiza elata</i>	99	20	12.91	4.92	38.1	24.10	3E-25

Species	N_f	N_i	Mean (mm)	SD	CV (%)	Individual Variation	
						F-value	P
<i>Daphne gnidium</i>	100	20	4.48	0.65	14.5	1.72	0.05
<i>Daphne laureola</i> ^G	101	20	6.65	3.86	57.9	37.46	3E-32
<i>Dipcadi serotinum</i>	77	20	8.84	1.73	19.6	4.09	19E-6
<i>Fedia cornucopiae</i>	100	20	12.44	4.23	34.0	16.40	3E-20
<i>Jasminum fruticans</i>	70	14	9.48	1.99	21.0	10.82	5E-11
<i>Lavandula latifolia</i>	100	20	6.86	0.71	10.4	6.87	3E-10
<i>Lavandula stoechas</i>	100	20	6.19	0.86	13.9	13.85	5E-18
<i>Linaria aeruginea</i>	124	28	20.54	2.51	12.2	12.17	1E-20
<i>Linaria anticaria</i>	78	20	19.84	2.72	13.7	4.61	33E-7
<i>Linaria viscosa</i>	93	20	15.56	2.32	14.9	5.59	36E-9
<i>Lithodora fruticosa</i>	97	20	8.82	2.03	23.1	6.83	4E-10
<i>Lonicera arborea</i>	100	20	4.99	0.99	19.8	4.87	24E-8
<i>Lonicera etrusca</i>	100	20	26.46	7.12	26.9	13.08	3E-17
<i>Lonicera implexa</i>	138	27	27.83	6.42	23.1	18.73	2E-29
<i>Lonicera splendida</i>	101	17	29.30	4.89	16.7	17.45	3E-20
<i>Marrubium supinum</i>	100	20	6.97	1.71	24.5	11.30	1E-15
<i>Mucizonia hispida</i>	96	20	8.56	1.33	15.5	6.93	4E-10
<i>Muscari comosum</i>	112	20	8.04	1.39	17.3	93.90	1E-51
<i>Narcissus cuatrecasasii</i>	30	30	15.13	1.49	9.8	—	—
<i>Origanum virens</i> ^G	150	30	6.36	2.26	35.5	35.41	7E-46
<i>Phlomis lychnitis</i>	100	20	25.39	2.46	9.7	10.02	3E-14
<i>Phlomis purpurea</i>	110	22	14.61	2.11	14.5	6.77	5E-11
<i>Pinguicula vallisneriifolia</i>	44	20	17.01	2.90	17.0	7.44	5E-6
<i>Pistorinia hispanica</i>	79	20	12.42	2.63	21.2	10.18	2E-12
<i>Polygala boissieri</i>	83	24	16.65	1.72	10.4	10.44	2E-13
<i>Primula vulgaris</i>	78	20	14.08	2.32	16.4	7.94	4E-10
<i>Prunella hyssopifolia</i>	81	18	10.03	1.04	10.4	3.40	21E-5
<i>Prunella laciniata</i>	113	19	11.69	1.61	13.7	20.85	3E-25
<i>Prunella vulgaris</i>	83	20	9.71	1.27	13.1	7.00	2E-9
<i>Rosmarinus officinalis</i>	100	20	6.01	1.06	17.6	7.43	5E-11
<i>Salvia argentea</i>	100	20	8.35	1.87	22.4	23.46	4E-25
<i>Salvia blancoana</i>	86	20	23.94	3.89	16.2	8.46	3E-11
<i>Salvia verbenaca</i>	58	12	8.12	1.88	23.2	11.46	7E-10
<i>Saponaria ocyroides</i>	100	20	11.85	1.24	10.5	3.64	26E-6
<i>Satureja intricata</i>	100	20	5.11	0.96	18.7	6.65	5E-10
<i>Scabiosa turolensis</i>	100	20	8.23	1.85	22.5	12.59	8E-17
<i>Sideritis arborescens</i>	65	13	7.11	1.24	17.4	20.16	2E-15
<i>Sideritis incana</i>	100	20	5.26	0.92	17.5	9.64	9E-14
<i>Silene colorata</i>	89	20	15.24	1.67	11.0	12.98	6E-16
<i>Silene lasiostyla</i>	53	20	18.98	2.62	13.8	14.34	7E-11
<i>Silene legionensis</i>	83	20	17.85	4.07	22.8	22.69	3E-21
<i>Silene vulgaris</i>	45	16	14.22	2.35	16.5	12.50	7E-9
<i>Teucrium rotundifolium</i>	100	20	10.14	1.47	14.5	5.29	54E-9
<i>Teucrium webbianum</i>	99	20	9.19	1.01	11.0	5.08	12E-8
<i>Thymus orospedanus</i> ^G	100	20	4.16	1.42	34.1	40.34	4E-33
<i>Trachelium caeruleum</i>	100	20	7.66	0.86	11.2	15.86	9E-20
<i>Viola cazorlensis</i>	80	20	29.60	7.34	24.8	13.28	6E-15

G = Gynodioecious, florally dimorphic species.

Acknowledgments

I am most grateful to J. Retana, J. Bosch, and X. Cerdá for generously supplying unpublished pollinator data, and S.C.H. Barrett, J. Herrera, P. Jordano, and two anonymous reviewers for constructive comments on earlier versions of the manuscript. J. Herrera and S. Talavera helped with some difficult plant identifications. My pollination studies in the Sierra de Cazorla were partly supported by grant PB87-0452 from the Dirección General de Investigación Científica y Técnica (DGICYT), and made possible by the facilities and permits provided by the Agencia de Medio Ambiente. While preparing this contribution, I was supported by grant PB91-0114 from DGICYT.

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