

SEXUAL DIMORPHISM IN FLOWER SIZE

LYNDA F. DELPH,¹ LAURA F. GALLOWAY,^{2,*} AND MAUREEN L. STANTON²¹Department of Biology, Indiana University, Bloomington, Indiana 47405; ²Section of Evolution and Ecology, Center for Population Biology, University of California, Davis, California 95616*Submitted April 23, 1995; Revised October 9, 1995; Accepted October 22, 1995*

Abstract.—Sexual dimorphism in the secondary characters of unisexual flowers is often observed. Most prior reports indicate that male flowers have larger petals than female flowers. In this article we examine hypotheses regarding patterns of perianth (sepals and petals) size dimorphism. (1) Developmental associations between the corolla and the stamens constrain the independent evolution of these characters. (2) The role of the perianth in enclosing the reproductive structures in the bud results in a correlation between the size of the enclosed structures and the perianth parts. (3) In animal-pollinated species, the perianth serves to attract pollinators; fitness gains achieved through allocation to attractive structures differ between the sexes. To test these hypotheses, we compared 919 species with unisexual flowers; quantitative measurements of floral parts were made for 84 of these species. Unlike most previous studies, this study found that the petals of male flowers were larger than those of females in less than one-half of the cases, demonstrating that developmental associations are not strictly responsible for patterns of sexual dimorphism. Relative perianth size appears to be evolutionarily labile, even within genera. Patterns of perianth-size dimorphism differed between temperate and tropical species and between animal- and wind-pollinated species. Perianth size was strongly associated with the size of the reproductive structures enclosed in each flower, suggesting that the function of petals and sepals to protect developing reproductive structures may determine their size. However, the size of the reproductive structures was a better predictor of perianth size in wind- than in animal-pollinated species, which supports the attractive function hypothesis of the perianth. We conclude that the two functional roles of the perianth, protection and attraction, are the primary determinants of perianth size in unisexual flowers.

Sexual dimorphism between males and females provided the major inspiration for Darwin's theory of evolution by sexual selection (Darwin 1871). In polygamous animals, males are often larger and/or showier than females, which led Bateman (1948) to hypothesize that greater variance in mating success among males in such populations has driven the evolution of their extreme secondary sexual characteristics. In contrast, he suggested that reproductive success in females is typically limited by resources rather than by mating success. Much later, Willson (1979) and Charnov (1979) pointed out that these same characteristics may apply to reproduction by flowering plants, and their arguments have inspired a host of theoretical and empirical studies of floral sex allocation and mating success (reviewed in Stephenson and Bertin 1983; Snow and Lewis 1993; Stanton 1994; Wilson et al. 1994).

Three principal lines of evidence have been used to argue that Bateman's prin-

* Present address: Department of Biology, Gilmer Hall, University of Virginia, Charlottesville, Virginia 22903.

ciple applies generally to plants. First, pollen supplementation experiments suggest that seed production is often, but not always, limited by resources, rather than by pollination (see Young and Young 1992 for a critical review of this literature, and Delph 1986). Second, several experimental studies have demonstrated that variation in floral attractiveness has a greater impact on components of male reproductive success than on seed production (Queller 1983; Bell 1985; Stanton et al. 1986, 1989; but see Galen 1989; Broyles and Wyatt 1990; Nilsson et al. 1992; Johnson et al. 1995). Third, in sexually dimorphic species, flowers containing pollen are often larger and showier than those lacking pollen (Darwin 1877; Knuth 1906; Baker 1948; Bell 1985). Recently, however, Wilson et al. (1994) have questioned the generality of the first two lines of evidence and have cautioned against the uncritical application of Bateman's principle to plants.

In this article, we investigate the underlying causes of sexual dimorphism in secondary floral characters, particularly the sepals and petals (the perianth), which Bell (1985) likened to the sexual displays of polygamous male animals. Because male and female roles are difficult to separate in cosexual plants, we have focused our attention on species in which the sexual functions are strictly segregated between flowers. Within limits set by genetic correlations between sexes, separation of sexual functions allows sexual dimorphism to evolve if male and female reproductive success are enhanced by different floral traits. Our goal is to characterize patterns of sexual dimorphism between male and female flowers and to determine the extent to which such differences are caused by selection on reproductive functions.

Historically, the observation that male flowers often have larger perianths than female flowers has been explained by both functional (adaptive) and nonfunctional (nonadaptive) hypotheses (Delph 1996). The functional hypotheses rest on the assertion that the larger perianth of male flowers confers a selective advantage, whereas the nonfunctional hypothesis argues that pleiotropic interactions between androecium size and corolla size limit the evolutionary flexibility of floral sex allocation patterns. On the basis of a broad comparative analysis, we address three specific questions in this article: (1) How common is this pattern of sexual dimorphism in flower size? (2) Does the pattern of floral dimorphism indicate that allocation to the petals is constrained by a developmental association with the stamens? (3) What do patterns of floral dimorphism suggest about the adaptive functions of the perianth in male and female flowers? If constraints common to many species dictate patterns of flower-size dimorphism, we expect a consistent difference in relative flower size independent of pollination system or perianth function. In contrast, if floral dimorphism is caused by sex-specific adaptations, then allocation patterns should reflect the functional roles of the petals and sepals. Below we outline the explicit predictions for each hypothesis.

Nonfunctional Hypotheses

There are at least three mechanisms that could dictate patterns of flower-size dimorphism that are independent of the function of the perianth. In the absence of selection, phylogenetic relatedness may cause patterns of dimorphism to be predicted better by ancestry than by function. Alternatively, there may be a lack

of genetic variation upon which selection can act, which would again cause patterns to be evolutionarily conservative. We do not test either of these explicitly, but the large number of diverse taxa we surveyed allows us to draw tentative conclusions based on the observed patterns of flower-size dimorphism across phylogenetic levels. Finally, it has been proposed that common developmental pathways may lead to associations or correlations between morphological traits (Riska 1986; Slatkin 1987). Such developmental correlations exist between flower parts (Lord 1981; Sachs 1988; Sattler 1988) and may prevent their independent evolution. We test this hypothesis, which we term the developmental correlation hypothesis.

Developmental correlation.—This hypothesis is predicated on the idea that strong developmental correlations between the stamens and the corolla lead to larger petal size in male flowers. Darwin (1877) was perhaps the first to hypothesize that petals of female flowers are smaller than those of flowers containing pollen, because of “a tendency to abortion spreading from the stamens to the petals” (p. 308). Other researchers also noticed the tendency of female flowers to be smaller and speculated that whatever mechanism inhibited the development of the androecium also suppressed the development of the petals (Baker 1948, 1957; van Nigtevecht 1966). One possible mechanism causing this correlation was identified by Plack (1957, 1958), who showed experimentally that removing anthers prior to the full development of the petals caused a reduction in petal size and that the full size of the petals could be restored by application of gibberellic acid. More recent studies have confirmed that hormones produced by the androecium are transported to the corolla, where they affect the corolla’s growth and pigmentation (Weiss and Halevy 1989; Weiss et al. 1990). If there is a consistent developmental association between the corolla and the stamens, we expect the corollas of male flowers to be consistently larger than those of female flowers, irrespective of taxon, pollination syndrome, or geographical region. For example, wind- and animal-pollinated species should show similar patterns of flower-size dimorphism (with male flowers, as a rule, being larger). Furthermore, there should be a correlation between androecium size and petal size among flowers within a species.

Functional Hypotheses

The functional hypotheses concern two independent functions of the floral perianth, namely, a protective or enclosing function and an attractive function. Both functions were first noted by Sprengel (translated and reprinted in Lloyd and Barrett 1996), but recent treatments have stressed the role of the perianth in attracting pollinators (e.g., Bell 1985). If allocation to sepals and petals is dictated by selection, then the patterns of variation should be related to one or both of these functions.

Protective or enclosing function.—This hypothesis predicts that the size of the perianth will be determined in part by the volume of the reproductive structures that it encloses in the bud (assuming that there is a correlation between the relative size of the parts at maturity and their size in the bud). Hence, male flowers with relatively large androecia should have a larger perianth than those with smaller androecia, not because of the amount of hormone produced per se,

but because the perianth encloses a larger volume. The pattern predicted by this hypothesis differs from that of the nonfunctional one: variation in the pattern of flower-size dimorphism should exist and should be related to the relative sizes of reproductive structures enclosed by the sepals and/or petals. For example, in species in which the gynoecium of female flowers is larger than the reproductive structures of the male flowers, perianths on female flowers should be larger than perianths on male flowers. If the size of the perianth is due principally to its protection function, then we expect that the correlation between the size of the perianth parts and the size of the structures enclosed by these parts should be consistent across pollination systems.

Attractive function.—This hypothesis is based on the premise that the morph whose mating success is more limited by access to mates should allocate more to attraction. The general prediction of this hypothesis is that perianth-size dimorphism should reflect whether or not the perianth parts act to attract pollinators. If Bateman's principle applies to outcrossing plants, we expect that males should allocate more to attraction than females (Bell 1985). Our expectations of flower-size dimorphism differ with mode of pollination: for animal-pollinated species, the attractive perianth organ on male flowers should be larger than that on female flowers, whereas among wind-pollinated species there should be no pattern. In addition, two other secondary characteristics of flowers, fragrance and nectar production, function unambiguously as advertisements and rewards for pollinators. Sexual dimorphism for these characters (e.g., Bawa and Opler 1975; Ågren et al. 1986; Delph and Lively 1992) would imply that selection for pollinator attraction acts more strongly in one sex than the other.

To distinguish between these hypotheses, we present analyses of two data sets. The first is qualitative, comparing relative sizes of perianths of male and female flowers from 919 monoecious and dioecious species, so that broad patterns of size dimorphism can be seen. The second is quantitative and includes measurements of specific floral parts made on male and female flowers from 84 species. Taken together, our results support the conclusion that both perianth functions determine to a large extent the relative size of male and female flowers and do not support the notion that floral allocation is evolutionarily conservative.

METHODS

Qualitative Data Set

Data on the relative size of parts of male and female flowers were compiled for 919 species (367 monoecious and 552 dioecious) from 102 families (see app. A). These data were obtained from measurements on fresh, preserved, and herbarium material, unpublished data, and published data in the literature, including floras. Each species was assigned to one of three categories with respect to perianth size: male > female, male = female, or female > male. The trait compared (referred to as "flower size" in some instances) was petal or tepal size (in 554 species, measured as length or area) unless they were lacking; in this case sepal size (or hypanthia) was compared. In order to test the developmental correlation

hypothesis, we analyzed the data set using only species with petals. Historically, petal length has been the trait most often measured (e.g., Baker 1948; Bell 1985). Data were also recorded for each species with regard to mode of pollination (either wind or animal pollinated) and region (either tropical or temperate). Flowers from two to 25 plants were measured for each sex in those cases involving fresh, preserved, or herbarium material. When quantitative measures were taken, means were compared and the sexes were categorized as being different in size only when the means differed by more than one standard error. Quality of size data from floras varied substantially, ranging from explicit perianth measurements for each sex to statements of the relative size of the sexes (e.g., "petals on male flowers larger than those on female flowers"). For example, a species might be said to have a perianth part ranging from 2 to 2.5 mm in female flowers and to 1 mm in male flowers, in which case it would be categorized as having female perianths $>$ male perianths. Misinterpretations of information from published flora may have occurred; however, misinterpretations would have led to species' being categorized as dimorphic in size, when in fact the two flower sexes are not statistically different in size. They are unlikely to have caused cases to be falsely categorized as $M > F$ when they were actually $F > M$, or vice versa.

Reducing nonindependence.—Phylogenetic relationships between the species included in the quantitative data set cause some of the 919 points to be statistically nonindependent (see Felsenstein 1985). For example, all of the species within a particular genus might show the pattern of male flowers to be larger than female flowers if the common ancestor showed this pattern, that is, if relative flower size were symplesiomorphic. To correct for any statistical nonindependence caused by this type of relationship, we applied a modification of the method suggested by Harvey and Mace (1982), which assumes that changes in character states within a genus are not independent and which reduces (but may not eliminate) nonindependence. This reduced the number of cases used in our analyses from 919 to 436. As an example, in a genus for which we had data on 10 species, if six species were categorized as $M > F$ and four species as $F > M$, then only one evolutionary change (i.e., change in character state) was assumed. In other words, only one case of $M > F$ and one of $F > M$ were included in the contingency tables, rather than 10 separate cases. Furthermore, if all genera of a particular family exhibited the same character state, the entire family contributed only one datum to the tables (unless there was a mixture of pollination syndromes and/or regions). This method was used in the analyses reported herein and is likely to be somewhat conservative for estimating the number of independent points; it should underestimate the number of character state changes. It is worth noting that the results are robust with respect to how nonindependence is reduced, in that two other very different methods gave us the same qualitative results. One alternative was to use all 919 cases. The other was highly conservative in that we assumed that changes in character states within a family are not independent. This reduced the number of cases to 296. Note that we do not attempt a formal phylogenetic reconstruction of the evolution of flower size, as the necessary data largely do not exist.

Quantitative Data Set

Measurements of several floral parts were made on 84 monoecious or dioecious species taken from fresh, preserved, or herbarium material or were taken from unpublished and published data (see app. B). Several of the preserved samples were provided by biologists in response to our request for material (see Acknowledgments). The data are biased with respect to region, with nearly 80% (67 species) coming from the temperate zone. Whenever possible, the following characters were obtained for each species: breeding system; mode of pollination; region (temperate zone or tropics); the number, color, showiness (yes or no), length, and width (and occasionally thickness) of petals, sepals, tepals, bracts, hypanthia, filaments, anthers, and styles (including stigma); corolla diameter; flower length; ovary length and width; position of ovary (superior or inferior); presence or absence (or quantity) of odor and nectar and the approximate number of flowers per inflorescence for each sex; and notation of what structures enclose the bud. The surface area of petals and sepals (or other perianth parts) was estimated by multiplying their length times width. While in some species petals appear to act primarily as attractants, in others the petals were the primary perianth part enclosing the developing reproductive structures, especially later in the development of the flower. Only species in which the perianth part that was compared enclosed, and therefore appeared to protect, reproductive structures at some point in the flower's development were included in analyses to contrast whether perianth size was controlled by the protective and/or attractive function. The volume of the reproductive structures enclosed by the perianth was calculated by multiplying the length by width by thickness by number of the structures enclosed (e.g., anthers for males and ovary for females if the ovary was superior). Reproductive structures that were not enclosed by a perianth, such as inferior ovaries, were not included in this volume measure.

Statistical Analysis

To test for associations between the relative size of male versus female flowers ($M > F$, $F > M$), region (temperate, tropical), and mode of pollination (animal, wind), the qualitative data were analyzed with logistic regression analysis for categorical variables (see, e.g., Horton et al. 1988). Variables were arranged to form a logit model, with relative size categories as the response variable. Hierarchical models were used to examine the relationship between the explanatory variables, region and mode of pollination, and the response variable (Trexler and Travis 1993). Likelihood-ratio tests of models with and without an explanatory variable (or interaction) were used to test the significance of the variable (e.g., a model with the interaction between relative size, region, and mode of pollination, relative to a simpler model with only the two-way interactions). These statistics are distributed as χ^2 . A significant three-way interaction is analogous to an interaction between region and mode of pollination in an ANOVA. Logit-model analyses were performed with the SPSSx statistical package. Contingency tables were constructed for a variety of comparisons of categorical data. These were evaluated with χ^2 (Yate's correction for continuity was applied when appropriate) or log-likelihood ratios.

An ANCOVA with the dependent variable M:F ratio of perianth size, the independent variable showiness (yes or no) of the perianth, and the covariate M:F ratio of the volume of reproductive parts enclosed by the perianth was performed on the quantitative data set with the statistical package SYSTAT. We applied a square-root transformation to M:F perianth size and a log-transformation to the M:F volume to meet the requirements of homogeneity of variances among groups. The assumption of parallel slopes was considered fulfilled when the interaction (between showiness and volume) was nonsignificant.

RESULTS

Qualitative Data Set

Sexual dimorphism in flower size appears to be a widespread phenomenon, occurring in all but three of the 102 families we investigated (see app. A). Overall, a flower-size dimorphism occurred in 85% of the 436 cases. The pattern or polarity of the dimorphism (i.e., $M > F$ or $F > M$) appears to be highly labile, with a substantial number of changes occurring at the generic level. Changes occurred in all orders for which data on more than one family had been collected, in 75% of the families with more than one genus represented, and in 48% of the genera with more than one species represented. For example, petals of females of *Ilex cymosa* (Aquifoliaceae) from Java are only about two-thirds the length of petals of males, whereas petals of females of *Ilex opaca* from North America are larger than those of males. Character changes within genera also occur on a more local level. Within the South Island of New Zealand, petals of females of *Plagianthus betulinus* (Malvaceae) are only 60% as long as those of males, whereas *Plagianthus divaricatus* has petals on females that are 111% the length of those of males.

The distribution of the 436 cases into each of the three flower-size categories, according to both region and mode of pollination, is presented in figure 1. Overall, 48% of the cases had larger male than female flowers and 37% had larger female than male flowers, with the remaining 15% showing no sexual dimorphism in flower size. The results of a logistic regression analysis of the percentage of cases in either the $M > F$ or $F > M$ categories revealed a significant interaction between region and mode of pollination (coefficient = 0.16, SE = 0.08). Likelihood-ratio tests of a model with the three-way interaction (between relative size, region, and mode of pollination) with a model that did not include the interaction revealed that including the three-way interaction significantly improved the fit ($\chi^2 = 4.14$, $df = 1$, $P = .042$). In other words, the likelihood of a case belonging to a specific size category depended on both the region and mode of pollination. Explicitly, species were considerably more likely to belong to the $M > F$ category if they were animal-pollinated temperate species than if they were animal-pollinated tropical species. Animal-pollinated species in the tropics were equally as likely to have larger female flowers than male flowers as they were to have larger male than female flowers. In contrast, the distribution of wind-pollinated species into the two categories did not differ by region: overall, about 60% of the wind-

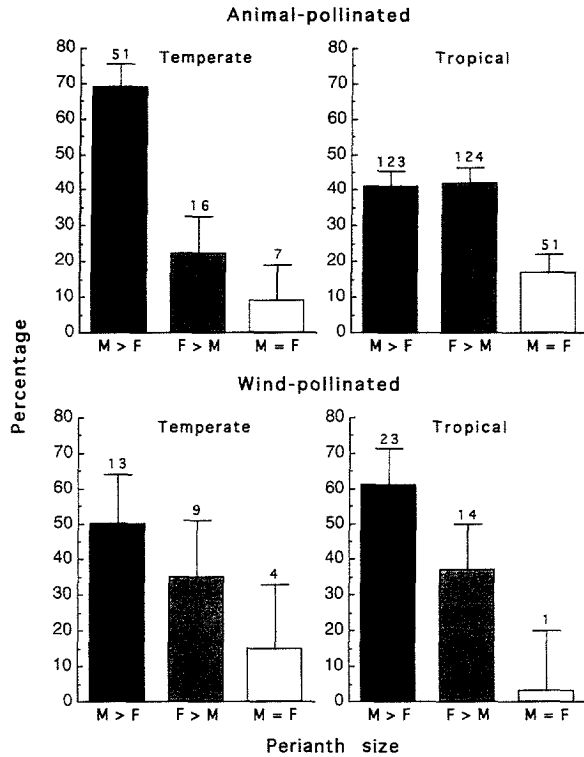


FIG. 1.—Percentage (\pm SE) of cases from the qualitative data set in which the perianth of males was larger than that of females ($M > F$), the perianth of females was larger than that of males ($F > M$), or they were approximately equal in size ($M = F$), for animal- and wind-pollinated flowering plant species from the temperate zone or the tropics (see text for which perianth part was compared). Numbers above each bar are the actual number of cases (either a species or a group of species) in each category.

pollinated cases had larger male than female flowers among those cases in which a size dimorphism existed.

The developmental correlation hypothesis is based on a phenotypic correlation between the stamens and the petals, so we also looked only at those species in which petal size was compared in order to test this hypothesis (e.g., eliminated species in which the perianth part compared was the sepals). Of the 298 cases, 50% had larger petals on male than female flowers, 37% had larger petals on female than male flowers, and 13% showed no sexual dimorphism in petal size.

Variation in the pattern of flower-size dimorphism suggests evolutionary lability of floral allocation patterns. Furthermore, the developmental correlation hypothesis is not supported, as petals on males are often smaller than those on females. The pattern of size dimorphism suggests that whatever the underlying developmental and/or phylogenetic associations are, significant variation in the relative size of the perianth parts is determined partly by the function of these parts.

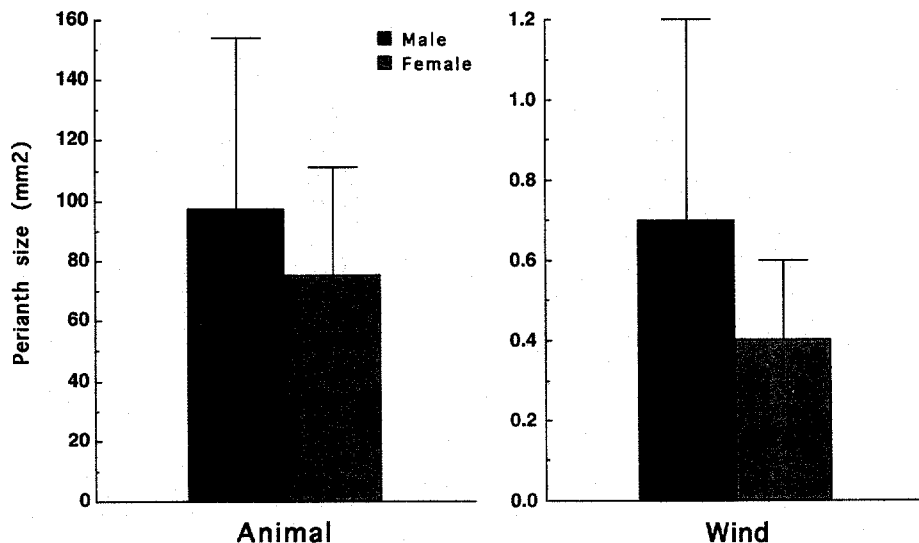


FIG. 2.— Mean (\pm SE) size (mm^2) of perianths of male and female flowers of animal- and wind-pollinated species from the quantitative data set. Note that the Y-axis differs in the two graphs and serves to hide the point of comparison. Perianths of both sexes are significantly larger in animal-pollinated than in wind-pollinated species (see text).

However, these results do not allow us to distinguish between the protection and the attractive function hypotheses.

Quantitative Data Set

Of the 84 mostly temperate species in the quantitative data set, 54 contained petals. Of these, male flowers had petals that were, on average, 1.55 (\pm 0.13 SE) times the size (in terms of area) of those on females, with approximately three-fourths of the species having larger petals on male than female flowers. For sepals, the average ratio of male to female sepal size was 1.41 (\pm 0.13), and sepals on male flowers were larger in 56% of the species ($N = 64$).

Comparison of secondary structures in animal- and wind-pollinated species suggests that perianth size is influenced by function. Analysis of the frequency of species having petals or showy sepals shows that animal-pollinated species are significantly more likely to have either petals (showy or not) or showy sepals (57 of 66 cases [86%]) than are wind-pollinated species (five of 18 cases [28%]; $\chi^2 = 22.2$, $P < .0001$). Moreover, the size of the perianth is much larger for animal-pollinated ($N = 66$) than wind-pollinated ($N = 18$) species for both males and females (see fig. 2; $t = 2.01$, $P = .049$ and $t = 2.33$, $P = .023$, respectively). Perianth parts compared were petals, if they were showy or if neither petals nor sepals were showy; otherwise, the size of the showy part was compared. Similar results are obtained if only the size of the petals is considered).

As with the qualitative data set, differences in secondary floral structures between the sexes depend on the mode of pollination. Animal-pollinated species

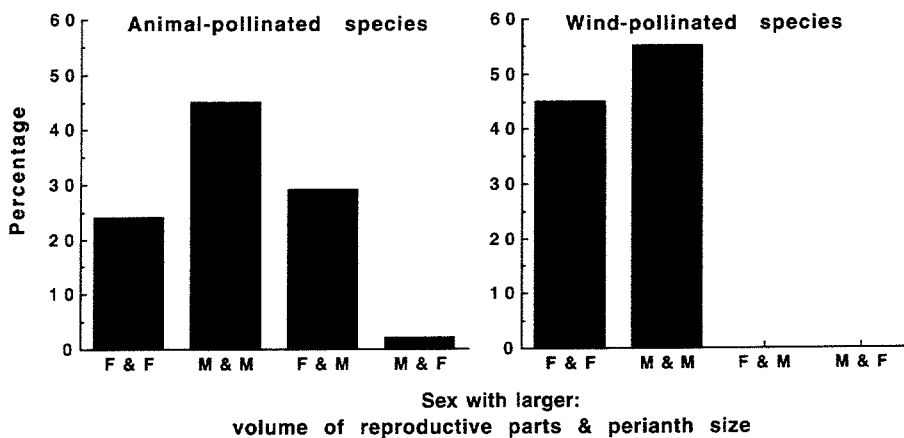


FIG. 3.—Comparison of dimorphism between the sexes for (1) volume of reproductive parts enclosed by the perianth until late in development and (2) the perianth size, for both animal- and wind-pollinated species (quantitative data set, $N = 42$ and 11 , respectively). The first letter in each category indicates which sex has a larger volume of enclosed parts, and the second letter indicates which sex has a larger perianth. For example, a species in the F & M category has larger volumes of reproductive structures to enclose in female flowers (hence, the first letter is F), but larger perianths on male flowers (hence, the second letter is M). Animal-pollinated species deviate significantly from what is expected if the protective function of the perianth is controlling the perianth-size dimorphism, because of a high percentage of species in the F & M category (see text).

are significantly more likely to have larger male than female perianths (51 of 65 cases [78%]), compared with wind-pollinated species (nine of 18 cases [50%]; $\chi^2 = 4.37$, $P = .037$).

For the temperate-biased quantitative data set, male perianths tend to be larger in both animal- and wind-pollinated species, suggesting that the pollinator attraction hypothesis alone cannot explain the pattern of size dimorphism. To determine whether this pattern is caused by the protective role of the perianth, we compared the relative size of the volume of enclosed reproductive structures and perianth parts jointly for each species. Each species was assigned to one of four categories, F & F, M & M, F & M, or M & F, in which the first letter indicates which sex had the larger volume of reproductive parts enclosed and the second letter indicates which sex had larger perianths. In a species assigned to category F & F, female flowers had both larger volumes enclosed and larger perianths than male flowers. In contrast, a species assigned to category F & M had larger volumes of reproductive structures enclosed on female than male flowers but larger perianths on male than female flowers. If the size of the perianth is controlled by the size of the reproductive parts enclosed by the perianth, species should be in the F & F or M & M categories. Animal-pollinated species show a distribution that is significantly different from this prediction (fig. 3; $G = 51.3$, $P < .001$). This difference is caused by 29% of the species exhibiting larger perianths on male flowers than female flowers even though the volume of the

reproductive parts enclosed is larger in female flowers (i.e., the F & M category). Because the relative size of the reproductive parts does not accurately predict perianth-size dimorphism, the protection hypothesis does not fully explain observed patterns in animal-pollinated species. In contrast, among wind-pollinated species, all species belong to either the F & F or M & M category (fig. 3). Hence, whether or not the relative size of the reproductive parts is a good predictor of relative perianth size appears to depend on whether the perianth also has an attractive function: it is a good predictor when the perianth does not have an attractive function and a relatively poor predictor when it does.

Does the protective function play any part in determining the relative size of the perianth parts among species whose perianths also have an attractive function? Within just the animal-pollinated species that have a showy perianth (either showy petals or showy sepals) that also acts to protect reproductive structures, there are 32 cases in which both the size of the showy part and the volume of the reproductive structures enclosed by that part is known. Nine species (28%) have larger perianths on females than males, and all nine of these species also have larger volumes of female than male reproductive parts enclosed. In contrast, of the 23 species (72%) that have larger perianths on males than females, only 10 of these have larger volumes of female than male reproductive parts. In other words, species having larger showy perianth parts on their female flowers also have larger female than male reproductive parts significantly more often than species that have larger showy perianth parts on their male flowers ($\chi^2 = 6.38$, $P < .012$). These results indicate that even when the perianth is functioning to attract pollinators, the relative size of the perianth parts is partially determined by the size of the reproductive parts they enclose.

An ANCOVA was performed to determine whether the male:female ratio of the size of perianth parts was affected by (1) whether or not either of the perianth parts were showy (yes or no) and/or (2) the M:F ratio of the volume of the reproductive parts enclosed (see table 1). The perianth part chosen for analysis varied among species and was chosen in the following order: (1) petals or sepals, depending on which was showy, or (2) petals if neither part was showy, or (3) sepals if neither part was showy and petals were absent (i.e., showy part first, then petals, then sepals). Both animal- and wind-pollinated species were included (but using only animal-pollinated species did not change the outcome). The ANCOVA indicated that showiness does not significantly affect the M:F ratio of the size of the perianth but that the M:F ratio of the volume of the reproductive parts has a significant effect (table 1). This result is graphed in figure 4, which shows that the M:F perianth ratio increases with the M:F volume of the reproductive parts enclosed.

Male-Female Comparisons for Other Aspects of Display and Reward

Investment in pollinator attraction and reward can take forms other than the production of a showy perianth. In addition to differences among males and females in the size of perianth parts, we also obtained data on the relative number of flowers produced per inflorescence, strength of floral fragrance or odor, and quantity of nectar produced for a subset of the animal-pollinated species. Data

TABLE 1

MEANS \pm SE OF THE MALE:FEMALE RATIO OF THE SIZE OF THE PERIANTH AND VOLUME OF THE REPRODUCTIVE STRUCTURES ENCLOSED BY THE PERIANTH

	PERIANTH SHOWY?	
	Yes (<i>N</i> = 49)	No (<i>N</i> = 35)
M:F perianth size	1.74 \pm .18	1.83 \pm .24
M:F volume of reproductive parts	2.70 \pm 1.15	5.61 \pm 3.08

NOTE.—See text for explanation of which perianth part was used. An ANCOVA, with the dependent variable M:F ratio of perianth size, revealed a nonsignificant effect of the effect of perianth showiness (MS [mean square] = .08, *df* = 1, *F* = .8, *P* = .38), a significant effect of the M:F ratio of the volume of reproductive parts enclosed (MS = 1.78, *df* = 1, *F* = 17.7, *P* < .001), and a nonsignificant interaction between showiness and volume (MS = .03, *df* = 1, *F* = .3, *P* = .61). Error MS = 10, *df* = 47; M:F perianth size was square-root transformed, and M:F volume of reproductive parts was log transformed prior to analysis.

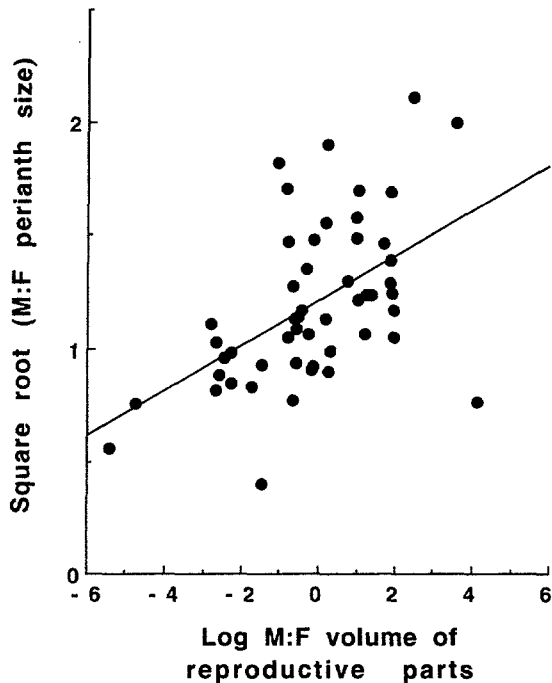


FIG. 4.—Relationship between the square root (male:female ratio of perianth size) and the log (male:female ratio of the volume of the reproductive parts enclosed by the perianth) ($r^2 = 0.27$, *N* = 51, from the quantitative data set).

from 50 species showed that males produce more flowers per inflorescence than females more often than expected by chance ($\chi^2 = 7.14$, $df = 1$, $P < .01$): there were 12 species with $M > F$, 36 with $M = F$, and two with $F > M$. Similarly, male flowers have a stronger odor than do females significantly more often than expected by chance ($\chi^2 = 7.14$, $df = 1$, $P = .01$): of 28 species, there were 12 with $M > F$, 14 with $M = F$, and only two with $F > M$. With regard to nectar, male flowers are equally as likely to produce more nectar than female flowers as female flowers are to produce more than male flowers (six species each with $M > F$ or $F > M$ and one with $M = F$).

DISCUSSION

We found that the majority of monoecious and dioecious species exhibit perianth-size dimorphism, and that, averaged across species in our data set with a dimorphism in perianth size, flowers on males are larger than those on females only 56% of the time. Here, we discuss our results in relation to the predictions of each of the hypotheses regarding the causal mechanisms of the pattern of dimorphism.

Nonfunctional Hypotheses

Developmental correlations between the androecium and the corolla of flowers are known to be mediated by hormones in some cases (Raab and Koning 1987; Weiss et al. 1990). Work with both experimental emasculations (Plack 1957, 1958; Weiss and Halevy 1989) and naturally occurring variation in androecium size and number in gynodioecious species has suggested that hormonal signals from anthers play a large part in determining the size of the corolla. For example, hermaphroditic flowers of gynodioecious *Geranium maculatum* (which has larger hermaphroditic than female flowers) with fewer than the normal complement of anthers have smaller petals than hermaphroditic flowers with full sets of anthers (Ågren and Willson 1991). If sufficiently invariant, this type of hormonal interaction could prevent the evolutionary modification of correlations between the size and/or presence of anthers and the size of the corolla, regardless of reproductive function. However, results of our study, as well as patterns of anther size and corolla size within species (see below), do not support the notion of a strict developmental correlation. Rather, it may be best to consider hormonal interactions evolved mechanisms that confer adaptive floral allocation patterns.

Rather than finding that perianths of male flowers are consistently larger than those of female flowers, we found variation in the relative size of male and female flowers. For the quantitative data set, petals on females were larger than those on males 25% of the time. For the qualitative data set, similar results were obtained whether only species with petals were included or all species in our data set were included: females had larger petals or perianths than males in 37%, irrespectively. Furthermore, we found an interaction between region and the mode of pollination for the pattern of dimorphism for the whole qualitative data set: male flowers of animal-pollinated species from the temperate zone were more likely to be larger than female flowers, whereas 49% of all of the species from

the tropics exhibiting flower-size dimorphism had larger female than male flowers. This is in striking contrast to past studies on flower-size dimorphism, all of which were largely based on temperate species, and all of which concluded that, *as a rule*, flowers containing pollen are bigger than female flowers (Darwin 1877; Knuth 1906; Baker 1948; Bell 1985). Our findings are, however, in accord with Bawa and Opler's (1975) finding that of the 20 dioecious, tropical species they investigated, 14 had larger female than male flowers.

Our most extreme quantitative case that went counter to the developmental hypothesis was that of *Marah fabacens* (Cucurbitaceae), an animal-pollinated, monoecious vine, in which female flowers had petals that were 2.4 times larger than those of male flowers. Interestingly, *Marah watsonii* showed the opposite pattern, having petals on female flowers that were only 0.6 times the size of those on males. This switch in the pattern of relative flower size among species within a genus is not unusual: we found such switches in nearly half of the genera for which we had information on more than one species. These switches within genera suggest that relative flower size is a highly labile trait.

Other examples and studies also support our contention that, although a developmental relationship between the androecium and corolla exists, it does not constrain allocation to floral structures, as the relationship can be altered by natural selection. For example, within several species of the genus *Viburnum*, the outer flowers within an inflorescence are sterile, containing neither pollen nor ovules. These flowers act to attract pollinators to the inflorescence (see Bell 1985) and, contrary to the developmental hypothesis, have much larger petals than the inner, fertile flowers. Similarly, anther size (and pollen production) is not positively correlated with petal size among 10 andromonoecious species of *Solanum*, in which the corolla is the attractive structure (Anderson and Symon 1989). Individuals of these species contain two types of flowers, male and hermaphroditic. We calculated the average male:hermaphrodite ratio of the size of the anthers and corolla size from data presented in Anderson and Symon's tables and found that although male flowers have slightly larger anthers on average than hermaphrodite flowers, their petals are only 0.79 times the size of petals on hermaphrodites. This goes counter to the expectation based on hormone production by the androecium as the primary factor controlling petal size. Finally, the results of an artificial selection experiment to break down the phenotypic correlation between pollen production and petal size in wild radish, *Raphanus sativus*, resulted in changing the correlation between them from a highly positive one to a weakly negative one, after only one generation (Stanton and Young 1994). Overall, these results do not support the hypothesis of a developmental correlation between the androecium and the corolla as a major factor controlling the pattern of sexual dimorphism in flower size of dioecious and monoecious species. Although strong hormonal interactions exist between flower parts, this should not be taken as evidence of a constraint on the evolution of flower size.

Functional Hypotheses

As predicted by the functional hypotheses, we found that variation in the pattern of perianth-size dimorphism was related to both the protective and attractive

functions of the perianth. We investigated this relationship by comparing the size of perianth parts and the volume of the reproductive structures enclosed by those parts, for wind- versus animal-pollinated species. It is commonly thought for wind-pollinated species that there should be an overall reduction in the size of the perianth parts, as they are essentially nonfunctional and should therefore be reduced for resource conservation and to avoid impeding pollen dispersal from the anthers and pollen capture by the stigmas (Faegri and van der Pijl 1979; Niklas 1982; Whitehead 1983). Our data support this view to some extent, in that we found that animal-pollinated species were more likely to have petals or showy sepals and also to have larger petals or sepals than wind-pollinated species. However, we do not adhere to the view that the perianth of wind-pollinated species is necessarily entirely nonfunctional, since it may enclose and protect the reproductive structures of the flowers during development.

The protective function hypothesis was supported by two lines of evidence. First, the volume of the reproductive structures enclosed by the perianth was a good predictor of perianth size among wind-pollinated species (see fig. 3). Furthermore, among animal-pollinated species whose perianths were showy (i.e., had both protective and attractive functions), all of those that had larger volumes of female reproductive parts also had larger female perianths, and the relative size of the perianth of males and females (M:F ratio of perianth size) was significantly and positively correlated with the relative volume of the parts enclosed.

The suggestion that the protective function of perianths might influence the relative size of male and female perianth parts was first made by Bawa and Opler (1975), who stated that the larger size of female flowers in the tropics relative to males might be caused by their bulky ovaries and larger nectaries (see also Feil 1992). This may be one reason why tropical species have a higher proportion of relatively large female flowers as compared to temperate species, but to test this directly, data on the volume of parts enclosed by the perianth are needed for more tropical species. Additional reasons for tropical patterns differing from those in the temperate zone have been proposed in an earlier study (Delph 1996). These include possible differences between geographical regions in the rewards offered to pollinators by the two sexes (females tend to lack rewards in the tropics; see Renner and Feil 1993) and differences in the floral sex ratio (possibly being more male skewed in the tropics; i.e., males are made attractive by their large number of flowers).

Our results also support the hypothesis that selection based on pollinator attraction affects floral dimorphism of males and females. We found that male flowers of animal-pollinated species, but *not* wind-pollinated species, were larger than those of females significantly more often than expected on the basis of relative size of the reproductive parts. However, the M:F ratio of the size of the perianth did not differ significantly between species with showy versus nonshowy perianths, as might be expected on the basis of the hypothesis that males should allocate more to attractiveness than females because female fitness is saturated with fewer pollinator visits than male fitness (see Bell 1985; Stanton and Galloway 1990; but see Wilson et al. 1994). However, attractiveness to pollinators may be affected by features other than just perianth size. Flower number, as well as

fragrance, could also differ between the sexes and affect their relative attractiveness to pollinators. If male fitness is more dependent on attractiveness than female fitness, then these traits should be enhanced in males relative to females, just as perianth size would be. In our quantitative, mostly temperate sample, we found that males of animal-pollinated species were likely to have significantly more flowers per inflorescence and to produce more fragrance per flower than females. Greater flower number in males than females has also been reported in several other studies (see reviews in Lloyd and Webb 1977; Bell 1985; Delph 1990, 1996), and pollinators have been found to respond to an increase in flower number by increasing their rate of visitation (Wyatt 1982; Schmid-Hempel and Speiser 1988; Thomson 1988).

We conclude that at least two reproductive functions, protection and pollinator attraction, have influenced the pattern of sexual dimorphism in flowers of dioecious and monoecious species. The historical, temperate-biased view that male perianths are typically larger than those on females is not supported by our larger comparative analysis that includes a large number of tropical species. For a number of potential, but still largely unexplored reasons, male and female fitness may tend to increase differently with allocation to attraction in tropical versus temperate regions. In addition, our results highlight the potential importance of the protective function of the perianth in determining flower size, a function that has been largely overlooked in the recent literature. Our investigation of allocation to secondary characters of unisexual flowers suggests that this allocation is labile and can be readily modified by natural selection.

ACKNOWLEDGMENTS

We dedicate this article to David Lloyd's inspiration and continuing recovery. We thank the many biologists who responded to our plea for data or samples of flowers, including G. Anderson, J. Antos, E. Bauder, P. Bierzychudek, C. Cid-Benevento, M. Cippolini, D. Costich, V. Delesalle, J. Dice, J. Fox, J. Kline, R. Lalonde, S. Mayer, T. Meagher, E. Menges, J. Reinartz, D. Waller, R. Zyskowski, and special thanks to P. Berry from the Missouri Botanical Garden. We thank C. Lively, J. Hill, L. McDade, and R. Shaw for comments on earlier versions of the manuscript. The research has been supported by National Science Foundation grants BSR-9010556 and DEB-9319002 to L.F.D. and BSR-8516333 to M.L.S., by Biomedical Research Support Grant RR07031-27 (from the Division of Research Resources, National Institutes of Health) to L.F.D., and University of California, Davis, graduate fellowships to L.F.G.

APPENDIX A

TABLE A1

LIST OF FAMILIES IN THE QUALITATIVE DATA SET AND THE NUMBER
OF GENERA AND SPECIES IN EACH

Family	Number of Genera	Number of Species
Aceraceae	1	1
Achariaceae	2	2
Alismataceae	1	2
Amaranthaceae	3	13
Anacardiaceae	9	25
Annonaceae	2	2
Apiaceae	2	2
Aquifoliaceae	1	2
Araliaceae	1	4
Asteraceae	9	14
Begoniaceae	1	21
Bixaceae	1	1
Brassicaceae	1	1
Bromeliaceae	1	1
Brunelliaceae	1	1
Burseraceae	5	22
Buxaceae	1	1
Cannabaceae	1	1
Caricaceae	1	1
Caryophyllaceae	1	3
Celastraceae	2	4
Ceratophyllaceae	1	1
Chenopodiaceae	1	1
Cornaceae	2	2
Corylaceae	2	2
Crassulaceae	2	2
Cucurbitaceae	21	30
Cyclanthaceae	3	4
Datiscaeeae	3	3
Dichapetalaceae	3	2
Dioscoreaceae	2	16
Ebenaceae	1	34
Elaeagnaceae	2	3
Elaeocarpaceae	1	2
Empetraceae	1	1
Epacridaceae	1	1
Ericaceae	1	1
Euphorbiaceae	56	178
Fabaceae	1	1
Fagaceae	9	64
Flacourtiaceae	8	20
Gnetaceae	1	5
Guttiferae	4	22
Hamamelidaceae	1	1
Hernandiaceae	1	3
Hydrocharitaceae	2	1
Icacinaceae	8	18
Juglandaceae	2	2
Lamiaceae	1	1
Lauraceae	6	12
Liliaceae	4	5

TABLE A1 (Continued)

Family	Number of Genera	Number of Species
Loranthaceae	4	6
Malvaceae	2	3
Meliaceae	2	4
Menispermaceae	12	15
Monimiaceae	4	5
Moraceae	14	14
Myricaceae	1	1
Myristicaceae	5	37
Myrsinaceae	2	3
Nepenthaceae	1	1
Nyctaginaceae	3	5
Nyssaceae	1	2
Oleaceae	1	1
Opiliaceae	1	1
Onagraceae	1	1
Orchidaceae	2	2
Palmae	34	54
Passifloraceae	2	6
Pittosporaceae	1	1
Plantaginaceae	1	1
Platanaceae	1	1
Polygonaceae	4	5
Proteaceae	1	1
Ranunculaceae	2	10
Restionaceae	1	1
Rhamnaceae	1	3
Rhizophoraceae	1	6
Rosaceae	4	7
Rubiaceae	6	14
Rutaceae	5	18
Salicaceae	1	18
Salvadoraceae	1	1
Santalaceae	1	1
Sapindaceae	3	3
Saxifragaceae	1	1
Schisandraceae	1	1
Scrophulariaceae	1	4
Scyphostegiaceae	1	1
Simaroubaceae	4	4
Smilacaceae	2	19
Solanaceae	1	1
Sparganinaceae	1	1
Sterculiaceae	4	4
Theligonaceae	1	1
Thymelaeaceae	3	16
Triuridaceae	1	1
Ulmaceae	5	19
Urticaceae	13	22
Valerianaceae	1	1
Violaceae	2	3
Vitaceae	2	6

NOTE.—Dimorphism occurred in all families except the Buxaceae and the Chenopodiaceae (for which we have data on only one species) and the Vitaceae (for which we have data on six species).

APPENDIX B

LIST OF SPECIES

The following is a list of species (given as family and genus and species) in the quantitative data set:

- Aceraceae:
Acer negundo
- Achariaceae:
Ceratiosicyos ecklonii
Guthriea capensis
- Alismataceae:
Sagittaria australis
Sagittaria montevidensis
- Anacardiaceae:
Astronium graveolens
Rhus glabra
Rhus typhina
- Annonaceae:
Anonidium mannii
- Apiaceae:
Aciphylla scott-thomsonii
- Aquifoliaceae:
Ilex opaca
- Asteraceae:
Antennaria parviflora
Antennaria rosulata
Baccharis pilularis
Cirsium arvense
Leptinella pyrethrifolia
Leptinella dendyi
Petasites frigidus
- Brassicaceae:
Lepidium sisymbroides
- Brunelliaceae:
Brunellia boliviana
- Caryophyllaceae:
Silene acaulis
Silene latifolia
- Cornaceae:
Griselinia littoralis
- Crassulaceae:
Rhodiola integrifolia
Sedum rosea
- Cucurbitaceae:
Cucurbita texana
Echallium elaterium
Marah fabacens
Marah watsonii
- Datiscaceae:
Datisca glomerata
- Elaeagnaceae:
Shepherdia canadensis
- Elaeocarpaceae:
Aristotelia fruiticosa
Aristotelia serrata
- Epacridaceae:
Cyathodes colensoi
- Euphorbiaceae:
Acalypha rhomboidia
Acalypha virginica
Tetracoccus dioicus
- Flacourtiaceae:
Xylosma benthamii
- Hernandiaceae:
Hernandia stenura
- Juglandaceae:
Juglans hindsii
- Lamiaceae:
Iboza riparia
- Lauraceae:
Lindera benzoin
- Liliaceae:
Chamaelirium luteum
- Loranthaceae:
Eremolepis schottii
Phoradendron flavescens
- Malvaceae:
Napaea dioica
Plagianthus divaricatus
Plagianthus betulinus
- Monimiaceae:
Monimia ovalifolia
- Moraceae:
Morus nigra
- Myrsinaceae:
Myrsine knudsenii
- Nepenthaceae:
Nepenthes alata
- Nyctaginaceae:
Guapira olfersiana
- Nyssaceae:
Nyssa sylvatica
- Oleaceae:
Fraxinus latifolia
- Onagraceae:
Fuchsia cylindracea
- Pittosporaceae:
Pittosporum acuminatum
- Platanaceae:
Platanus racemosa

APPENDIX B (Continued)

- Polygonaceae:
Rumex acetosella
Muehlenbeckia australis
- Ranunculaceae:
Clematis afoliata
Clematis foetida
Thalictrum dioicum
- Restionaceae:
Leptocarpus similis
- Rosaceae:
Fragaria chiloensis
Oemleria cerasiformis
Rubus chamaemorus
Rubus cissoides
- Rubiaceae:
Coprosma robusta
Coprosma lucida
Galium nuttallii
Galium perpusillum
- Rutaceae:
Melicope simplex
Pelea clusiaefolia
Zanthoxylum americanum
- Sapindaceae:
Dodonaea viscosa
- Smilacaceae:
Smilax auriculata
- Solanaceae:
Solanum appendiculatum
- Theaceae:
Eurya sandwicensis
- Thymelaeaceae:
Pimelea traversii
Wikstroemia pulcherrima
- Urticaceae:
Pilea pumila
Urtica ferox
- Violaceae:
Melicytus ramiflorus

LITERATURE CITED

- Ågren, J., and M. F. Willson. 1991. Gender variation and sexual differences in reproductive characters and seed production in gynodioecious *Geranium maculatum*. *American Journal of Botany* 78:470–480.
- Ågren, J., T. Elmqvist, and A. Tunlid. 1986. Pollination by deceit, floral sex ratios and seed set in dioecious *Rubus chamaemorus* L. *Oecologia* (Berlin) 70:332–338.
- Anderson, G. J., and D. E. Symon. 1989. Functional dioecy and andromonoecy in *Solanum*. *Evolution* 43:204–219.
- Baker, H. G. 1948. Corolla size in gynodioecious and gynomonoeious species of flowering plants. *Proceedings of the Leeds Literary and Philosophical Society* 5:136–139.
- . 1957. Expression of sex in flowering plants. *Nature* (London) 180:614–615.
- Bateman, A. J. 1948. Intrasexual selection in *Drosophila*. *Heredity* 2:349–369.
- Bawa, K. S., and P. A. Opler. 1975. Dioecism in tropical trees. *Evolution* 29:167–179.
- Bell, G. 1985. On the function of flowers. *Proceedings of the Royal Society of London B* 224:223–265.
- Broyles, S. B., and R. Wyatt. 1990. Paternity analysis in a natural population of *Asclepias exaltata*: multiple paternity, functional gender, and the "pollen-donation hypothesis." *Evolution* 44:1454–1468.
- Charnov, E. L. 1979. Simultaneous hermaphroditism and sexual selection. *Proceedings of the National Academy of Sciences of the USA* 76:2480–2484.
- Darwin, C. 1871. *The descent of man, and selection in relation to sex*. J. Murray, London.
- . 1877. *The different forms of flowers on plants of the same species*. J. Murray, London.
- Delph, L. F. 1986. Factors regulating fruit and seed production in the desert annual *Lesquerella gordonii*. *Oecologia* (Berlin) 69:471–476.
- . 1990. Sex-differential resource allocation patterns in the subdioecious shrub *Hebe subalpina*. *Ecology* 71:1342–1351.
- . 1996. Flower size dimorphism in unisexual plants. Pages 217–237 in D. G. Lloyd and S. C. H. Barrett, eds. *Floral biology: studies on floral evolution in animal-pollinated plants*. Chapman & Hall, New York.
- Delph, L. F., and C. M. Lively. 1992. Pollinator visitation, floral display, and nectar production of the sexual morphs of a gynodioecious shrub. *Oikos* 63:161–170.

- Faegri, K., and L. van der Pijl. 1979. Principles of pollination ecology. 3d ed. Pergamon, Oxford.
- Feil, J. P. 1992. Reproductive ecology of dioecious *Siparuna* (Monimiaceae) in Ecuador: a case of gall midge pollination. *Botanical Journal of the Linnean Society* 110:171–203.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.
- Galen, C. 1989. Measuring pollinator-mediated selection on morphometric floral traits: bumble bees and the alpine sky pilot, *Polemonium viscosum*. *Evolution* 43:882–890.
- Harvey, P. H., and G. Mace. 1982. Comparisons between taxa and adaptive trends: problems of methodology. Pages 343–361 in King's College Sociobiology Group, eds. *Current problems in sociobiology*. Cambridge University Press, Cambridge.
- Horton, D. R., J. L. Capinera, and P. L. Chapman. 1988. Local differences in host use by two populations of the Colorado potato beetle. *Ecology* 69:823–831.
- Johnson, S. G., L. F. Delph, and C. L. Elderkin. 1995. The effect of petal-size manipulation on pollen removal, seed set, and insect-visitor behavior in *Campanula americana*. *Oecologia* (Berlin) 102:174–179.
- Knuth, P. 1906. *Handbook of flower pollination*. Vol. 1. Clarendon, Oxford.
- Lloyd, D. G., and S. C. H. Barrett, eds. 1996. *Floral biology: studies on floral evolution in animal-pollinated plants*. Chapman & Hall, New York.
- Lloyd, D. G., and C. J. Webb. 1977. Secondary sex characters in plants. *Botanical Review* 43:177–216.
- Lord, E. M. 1981. Cleistogamy: a tool for the study of floral morphogenesis, function and evolution. *Botanical Review* 47:421–449.
- Niklas, K. J. 1982. Pollination and airflow patterns around conifer ovulate cones. *Science* (Washington, D.C.) 217:442–444.
- Nilsson, L. A., E. Rabakonandrianina, and B. Peterson. 1992. Exact tracking of pollen transfer and mating in plants. *Nature* (London) 360:666–667.
- Plack, A. 1957. Sexual dimorphism in Labiatae. *Nature* (London) 180:1218–1219.
- . 1958. Effect of gibberellic acid on corolla size. *Nature* (London) 182:610.
- Queller, D. C. 1983. Sexual selection in a hermaphroditic plant. *Nature* (London) 305:706–707.
- Raab, M. M., and R. E. Koning. 1987. Changes in responsiveness to ethylene and gibberellin during corolla expansion of *Ipomoea nil*. *Journal of Plant Growth Regulation* 6:121–131.
- Renner, S. S., and J. P. Feil. 1993. Pollinators of tropical dioecious angiosperms. *American Journal of Botany* 80:1100–1107.
- Riska, B. 1986. Some models for development, growth, and morphometric correlation. *Evolution* 40:1303–1311.
- Sachs, T. 1988. Ontogeny and phylogeny: phytohormones as indicators of labile changes. Pages 157–176 in L. D. Gottlieb and S. K. Jain, eds. *Plant evolutionary biology*. Chapman & Hall, New York.
- Sattler, R. 1988. Homeosis in plants. *American Journal of Botany* 75:1606–1617.
- Schmid-Hempel, P., and B. Speiser. 1988. Effects of inflorescence size on pollination in *Epilobium angustifolium*. *Oikos* 53:98–104.
- Slatkin, M. 1987. Quantitative genetics of heterochrony. *Evolution* 41:799–811.
- Snow, A. A., and P. O. Lewis. 1993. Reproductive traits and male fertility on plants: empirical approaches. *Annual Review of Ecology and Systematics* 24:331–351.
- Stanton, M. L. 1994. Male-male competition during pollination in plant populations. *American Naturalist* 144:S40–S68.
- Stanton, M. L., and L. F. Galloway. 1990. Natural selection and allocation to sexual reproduction in flowering plants. *Lectures on Mathematics in the Life Sciences* 22:1–50.
- Stanton, M. L., and H. J. Young. 1994. Selecting for floral character associations in wild radish, *Raphanus sativus* L. *Journal of Evolutionary Biology* 7:271–285.
- Stanton, M. L., A. A. Snow, and S. N. Handel. 1986. Floral evolution: attractiveness to pollinators increases male fitness. *Science* (Washington, D.C.) 232:1625–1627.
- Stanton, M. L., A. A. Snow, S. N. Handel, and J. Berezky. 1989. Effects of a flower color polymorphism upon mating patterns in experimental populations of wild radish, *Raphanus raphanistrum*. *Evolution* 43:335–346.
- Stephenson, A. G., and R. I. Bertin. 1983. Male competition, female choice, and sexual selection

- in plants. Pages 109–149 in L. Real, ed. *Pollination biology*. Academic Press, Orlando, Fla.
- Thomson, J. D. 1988. Effects of variation in inflorescence size and floral rewards on the visitation rates of traplining pollinators of *Aralia hispida*. *Evolutionary Ecology* 2:65–76.
- Trexler, J. C., and J. Travis. 1993. Nontraditional regression analysis. *Ecology* 74:1629–1637.
- van Nigtevecht, G. 1966. Genetic studies in dioecious *Melandrium*. I. Sex-linked and sex-influenced inheritance in *Melandrium album* and *Melandrium dioicum*. *Genetica* 37:281–306.
- Weiss, D. W., and A. H. Halevy. 1989. Stamens and gibberellin in the regulation of corolla pigmentation and growth in *Petunia hybrida*. *Planta* 179:89–96.
- Weiss, D., A. J. van Tunen, A. H. Halevy, J. N. M. Mol, and A. G. M. Gerats. 1990. Stamens and gibberellic acid in the regulation of flavonoid gene expression in the corolla of *Petunia hybrida*. *Plant Physiology* 94:511–515.
- Whitehead, D. R. 1983. Wind pollination: some ecological and evolutionary perspectives. Pages 97–109 in L. Real, ed. *Pollination biology*. Academic Press, Orlando, Fla.
- Willson, M. F. 1979. Sexual selection in plants. *American Naturalist* 113:777–790.
- Wilson, P., J. D. Thomson, M. L. Stanton, and L. P. Rigney. 1994. Beyond floral Batemanian: gender biases in selection for pollination success. *American Naturalist* 143:283–296.
- Wyatt, R. 1982. Inflorescence architecture: how flower number, arrangement, and phenology affect pollination and fruit-set. *American Journal of Botany* 69:585–594.
- Young, H. J., and T. P. Young. 1992. Alternative outcomes of natural and experimental high pollen loads. *Ecology* 73:639–647.

Associate Editor: Ruth G. Shaw