

# TESTING HYPOTHESES OF FUNCTIONAL RELATIONSHIPS: A COMPARATIVE SURVEY OF CORRELATION PATTERNS AMONG FLORAL TRAITS IN FIVE INSECT-POLLINATED PLANTS<sup>1</sup>

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To test hypotheses on the evolution of functional relationships, phenotypic correlations among floral traits were estimated in five species of insect-pollinated plants. The species studied were wild radish (*Raphanus raphanistrum*), canola (*Brassica napus*), phlox (*Phlox divaricata*), dame's rocket (*Hesperis matronalis*), and black mustard (*Brassica nigra*). Six floral traits were measured on each species. In three of the five species the correlations between the filaments and corolla tube were significantly greater than the other floral correlations. This result is consistent with the hypothesis that selection for proper anther placement to enhance pollination has increased the filament–corolla tube correlations in these three species. In contrast, none of the species showed evidence of selection for an optimal stigma placement; the correlations between the pistil and corolla tube lengths were not greater than the other floral correlations in any of the five species.

Organisms are not collections of independent traits. Groups of traits must work together as organs to perform essential functions, and these organs must in turn work together in organ systems to produce an organism that is adapted to its environment. A major unresolved question in evolutionary biology is how genetic, developmental, and phenotypic relationships among different traits evolve to produce functionally integrated organs or organisms. One approach to answering this question is to examine the evolution of phenotypic and genetic correlations among traits (Olsen and Miller, 1958; Cheverud, 1982, 1984). Selection on the correlation between traits can occur when certain combinations of trait values confer higher fitness than other combinations. Given adequate genetic variance, this selection can in turn alter the correlations over evolutionary time. Very little empirical evidence concerning the evolution of correlations exists, but a few studies demonstrate selection for increased correlation between traits that are functionally related (Arnold and Bennett, 1988; Moore, 1990; Brodie, 1992). On the other hand, some traits or groups of traits may function more effectively if they are decoupled from each other, so that they vary independently (Berg, 1960).

One way to study the evolution of correlations is to look for evidence of past selection in present-day correlation patterns (Berg, 1960; Kingsolver and Wiernasz, 1987, 1991; Armbruster, 1991; Conner and Via, 1993). Based on patterns of correlations among morphological traits in wild radish, Conner and Via (1993) hypothesized that pollinators might have caused selection for increased

integration among floral traits. Here we report tests of this hypothesis.

The hypothesis of selection for increased integration concerned the placement of the anthers and stigma relative to the opening of the corolla tube for effective pollination. Conner and Via (1993) predicted that the filament and corolla tube lengths of wild radish flowers should be similar to each other regardless of the overall size of the flower, because this relationship places the anthers at the opening of the corolla tube. For a plant like wild radish that is visited by insects of various sizes (see below), this anther position may be a particularly effective way to place pollen on a variety of different-sized pollinators, without the flower necessarily matching the size of the pollinator. Related arguments have been made by Grant and Grant (1965) and Harder and Barrett (1993). We expected that this integration of filament and corolla tube lengths would be manifested as a high phenotypic correlation between the two traits. The results for wild radish were consistent with this prediction: phenotypic and genetic correlations between the filaments and corolla tube exceeded the correlations among the other pairs of floral traits (Conner and Via, 1993).

In contrast, an analogous prediction for female function, that the pistil and corolla tube lengths should also be highly correlated to maintain effective positioning of the stigma relative to the corolla tube opening, was not supported: the pistil–corolla tube correlation was no higher than the background level of floral correlations in wild radish (Conner and Via, 1993). This result, coupled with the higher filament–corolla tube correlation, suggested either that the adaptive hypotheses were wrong or that selection on floral morphology acted more strongly through male function than female function.

Three conditions must be met for us to expect the evolution of increased filament–corolla tube or pistil–corolla tube correlations. First, the flower must have a narrow tubular portion, which restricts pollinators' access to the nectaries and places the anthers close to each other at the center of the flower. This forces pollinators of any size

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TABLE 1. Species studied, with location collected, grown, and number of individuals measured. The location grown column is blank for species measured from naturally occurring populations and the collected column is blank for canola because it was grown from commercial seed. All locations other than NY and MI were near Urbana, IL; the MI and NY seeds were each collected from single large populations.

Species	Collected	Grown	N	Year
<i>Raphanus raphanistrum</i> (Wild radish, Brassicaceae)	NY	Greenhouse	340	1989
	MI	Greenhouse	110	1992
	NY	Phillips Tract	57	1991
	NY	Phillips Tract	65	1992
<i>Brassica napus</i> (Canola, Brassicaceae)	—	Phillips Tract	50	1991
<i>Phlox divaricata</i> (Phlox, Polemoniaceae)	Trelease Woods	—	50	1991
<i>Hesperis matronalis</i> (Dame's rocket, Brassicaceae)	Phillips Tract	—	50	1991
<i>Brassica nigra</i> (Black mustard, Brassicaceae)	Junkyard	—	50	1991
	Clearing	—	47	1992
	Large	—	48	1992
	Junkyard	Phillips Tract	43	1992

to go to the opening of the corolla tube, regardless of whether they are foraging for nectar or pollen. Secondly, pollen must be placed on the pollinator's body instead of the proboscis. If the anthers and stigma are deeply inserted into the corolla tube, then the flower is likely to be primarily proboscis-pollinated. In this case the precise position of the anthers and stigma relative to the corolla tube opening should not matter; they need only to be placed somewhere above the nectaries, so that the proboscis will always pass them on the way to the nectar. Finally, plant fitness must be increased by increased pollen removal from the anthers (for the filament-corolla tube correlation) and by increased deposition on the stigma (for the pistil-corolla tube correlation). Note that these hypotheses do not address the positions of the stigma and anthers relative to each other; there are a number of ways in which the relative positions of stigmas and anthers can affect pollination (e.g., Thomson and Stratton, 1985; Harder and Barrett, 1993).

One alternative to these selective hypotheses is that the correlation patterns observed are caused by general angiosperm developmental patterns that have not been altered by selection for effective pollination. In fact, studies of floral development suggest that the stamens and petals are more closely linked in development than are other floral structures (Hill and Lord, 1989 and references therein). This developmental relationship between the stamens and petals could result in strong filament-corolla tube correlation. If this developmental hypothesis were correct, then one would expect consistent correlation patterns across taxa, particularly among closely related species. If, on the other hand, correlations have been altered by selection, then the correlation patterns should reflect other differences among the taxa, such as differences in morphology or pollination systems. Berg (1960) provided such evidence for correlations between floral and vegetative traits, showing that correlation patterns were related to the pollination systems of the species studied.

The goal of this study was to test the hypotheses of selection for functional integration between the filament and corolla tube and between the pistil and corolla tube for effective pollination, using a comparative survey of phenotypic correlation patterns among five plant species. The flowers of two of the species, wild radish and canola,

fit the conditions of the selective hypotheses listed above, while the other three do not. Phlox and dame's rocket have deeply inserted anthers (see Results) and are likely to be largely or exclusively proboscis pollinated (this has been suggested previously for phlox [Grant and Grant, 1965; Levin and Berube, 1972]), while black mustard does not have a narrow corolla tube. Therefore, if the selective hypotheses are correct, we expect higher filament-corolla tube and pistil-corolla tube correlations in wild radish and canola and not in phlox, dame's rocket, or black mustard. If selection has not altered correlations, all species should show similar patterns. Note that these predictions are based on only a few morphological features of the flowers and ignore many other facets of the pollination biology of these species.

## MATERIALS AND METHODS

**Species studied**—We chose the five species studied (Table 1) based on two main criteria. First, their floral morphologies are sufficiently similar that the same traits could be measured. Second, they were available near Urbana, IL. Four of the species are annuals in the Brassicaceae. Canola (*Brassica napus*) is an oil-seed crop, and black mustard (*Brassica nigra*), wild radish (*Raphanus raphanistrum*), and dame's rocket (*Hesperis matronalis*) are widespread weeds of disturbed areas. Within the Brassicaceae, the genera *Brassica* and *Raphanus* are very closely related, while *Hesperis* is less closely related to the other two (Hedge, 1976). The final species is *Phlox divaricata* (Polemoniaceae), a spring woodland perennial.

The flowers of all these species are visited by a variety of bees, butterflies, and flies, and the pollinator composition of the four Brassicaceae species are similar (Grant and Grant, 1965; Free, 1970; Kay, 1976; Stanton et al., 1989; J. Conner et al., unpublished data, University of Illinois). *Phlox divaricata* is visited and pollinated effectively only by very long-tongued insects, whereas the four Brassicaceae are pollinated by both short- and long-tongued insects. The taxonomic composition of visitors to wild radish and black mustard varies greatly in space and time (Stanton et al., 1991; Conner and Neumeier, 1995). Extensive spatial and temporal variability in visitation seems normal for plants visited by diverse insect

pollinators (e.g., Herrera, 1988; Eckhart, 1992); therefore, all the species in our study are likely to experience variability in the taxonomic composition of visitors.

Wild radish and black mustard are obligate outcrossers, being almost entirely self-incompatible (Sampson, 1964; Free, 1970; Stanton et al., 1989; J. Conner, unpublished data, University of Illinois). *Phlox divaricata* is partially self-compatible, but seed set is greatly increased by out-crossing and insect visitation is required for self-fertilization (Willson, Miller, and Rathcke, 1979). *Brassica napus* is self-compatible, but seed set and germination of the seeds produced are increased by insect visitation (Free, 1970; Fries and Stark, 1983; Kevan and Eisikowitch, 1990). Therefore, effective insect pollination is crucial for these four species. To our knowledge, the mating system of dame's rocket is unknown, although it is probably self-compatible (L. Delph, personal communication, Indiana University).

Eleven natural, garden, greenhouse, or agricultural populations of the five species were studied (Table 1). The experimental populations (all of the wild radish populations and one of the black mustard populations) were all grown from seeds collected in natural populations. Wild radish seeds were collected in New York and Michigan because we have found only one very small population of this species in central Illinois. Seeds used for experimental populations or plants measured in natural and agricultural populations were sampled in the same way: one plant was sampled every 1–2 m along transects or grids (depending on the size and shape of the population). In the experimental populations, only one randomly chosen offspring from each field maternal parent was grown. The canola plants were from an agricultural field planted with an open-pollinated commercial variety ('Cascade', Calgene, Inc., Leesburg, GA).

**Traits measured**—One to three flowers were measured on each plant; if more than one flower was measured, the mean values for each plant were used. Six floral traits were measured on plants in all populations studied: the length and width of the distal, showy part of the petal (the "limb," outside the corolla tube), the length of the corolla tube (the "claw," the proximal part of the petal), the length of the pistil, and the lengths of the longest and shortest filaments. Note that what we refer to as the corolla tube is not a true tube in the four species of Brassicaceae because the corolla is not fused. However, in all but black mustard, the petals and sepals are erect, forming a functional corolla tube that controls the access of pollinators to the nectaries (which are at the base of the tube). All Brassicaceae have two short filaments and four long filaments; in the species we studied, there was very little variation in length within the two length classes. *Phlox* has a true fused corolla tube with five filaments of varying lengths that are partially fused to the tube, and thus provides a useful comparison of an unrelated species that is convergent in general floral form with the species of Brassicaceae, but differs in several details of floral morphology. The full lengths of the shortest and longest *phlox* filaments were measured, including the portion that is fused to the corolla tube.

In the three populations of wild radish grown from New York seeds, flowers that opened after 1600 hr were

measured the next day. All other populations were measured with no knowledge of floral age, so that any ontogenetic changes in floral traits were not controlled for. If dimensions of different traits change at different rates, this would tend to reduce the correlations among the traits. In wild radish, the pistil elongates throughout the floral period, but dimensions of all other traits remain essentially constant from anthesis until wilting (J. Conner, unpublished data, University of Illinois).

Flowers of all wild radish populations, *phlox*, and the black mustard population grown at the Phillips Tract were measured *in situ* in the greenhouse or field. For canola, dame's rocket, and the three natural populations of black mustard, inflorescences or whole plants were cut, the cut ends placed immediately in water, and transported back to the laboratory within 30 min of cutting for measurements. No visible wilting of these plants occurred before measurements were made. All traits were measured with digital calipers, and measurement errors for all traits were <2% (for details on measurement error estimation see Conner and Via, 1993).

**Data analyses**—Phenotypic correlations among traits were calculated as Pearson product-moment correlations. The phenotypic correlations investigated in this study are appropriate for evaluating these selective hypotheses because the phenotype determines fitness and adaptation. For example, whether the anthers are placed at the same location relative to the opening of the corolla tube in all individuals is determined by the phenotypic correlation between filament and corolla tube.

To test the functional hypotheses outlined above, two paired subsets of the correlations were compared in each species, one pair for the male function and one for the female function hypotheses. For male function the two correlations between the corolla tube and the two filaments (short and long) were used. The correlation between the pistil and corolla tube was used to test the female-function hypothesis. These correlations were compared (see below) to the mean of the remaining 11 floral correlations, which represents the general background level of correlation among the floral traits. If the selection hypotheses are correct, then the filament-corolla tube correlations and the pistil-corolla tube correlation should be significantly greater than the rest of the floral correlations. The correlation between the short and long filaments was left out of these comparisons entirely because it was not clear to which group it belonged. The selective hypotheses make no clear prediction about this correlation, so this correlation does not fit into the group predicted to be higher due to selection. Conversely, the filament lengths are different forms of the same trait, unlike all the other traits, so the correlation between them is not a good indicator of general correlations among different traits in the flower.

Four of the five species studied were in the family Brassicaceae; therefore, if the same pattern of correlation is found in all four species, then this result could be due to shared ancestry. However, differences in correlation patterns among these species in the same family would suggest that the correlations have diverged through evolution.

The two sets of comparisons outlined above each in-

volve comparing subsets of correlations from the same correlation matrix; therefore, the correlations being compared are not independent and standard statistical tests are inappropriate. For this reason, a bootstrap analysis (Efron, 1982) was performed using SAS (SAS, 1989). For each bootstrap resampling, a random sample of individual plants was drawn with replacement until the sample size matched the total number of plants in that population (see Table 1). Therefore, the units being resampled were individual plants, which are likely to be independent (see sampling procedures above), rather than variables within plants, which are not independent. Pearson product-moment correlations were calculated and then Fisher's  $z$ -transformation was used to improve normality (Snedecor and Cochran, 1989). The two groups of correlations were then compared using an unpaired  $t$ -test. This entire procedure was repeated 200 times, generating 200  $t$ -statistics. If the mean of the 200  $t$ -statistics  $\pm 2$  SD failed to overlap zero, then the difference between the groups of correlations was judged to be significant. The use of standard deviations in the significance criterion assumes that the  $t$ -statistics are distributed normally. While some deviation from normality was seen, using percentiles instead of standard deviations gave the same qualitative results.

## RESULTS

The mean lengths of the three floral traits most crucial to the adaptive hypotheses are presented in Fig. 1. Note that wild radish and phlox had the largest flowers, canola and dame's rocket were intermediate, and black mustard was the smallest. These data also show that phlox and dame's rocket have deeply inserted anthers and stigmas and therefore are not predicted to have increased filament-corolla tube and pistil-corolla tube correlations (see Introduction).

The correlations between the filaments and the corolla tube were significantly higher than the background level of floral correlation in wild radish (all four populations), canola, and phlox (Fig. 2). The filament-corolla tube correlations were not significantly different than the rest of the floral correlations in dame's rocket and black mustard (all four populations).

In contrast to the filament-corolla tube results, the correlation between the pistil and corolla tube was never significantly greater than the background floral correlations (Fig. 3). The only significant difference was in dame's rocket, in which the pistil-corolla tube correlation was significantly lower than the mean background floral correlation.

## DISCUSSION

The correlation patterns reported here are consistent in two ways, suggesting that these are not ephemeral patterns but robust phenomena requiring explanation. First, the filament-corolla tube patterns are extremely consistent across the four field and greenhouse populations of wild radish, all of which exhibited filament-corolla tube correlations that were significantly greater than the rest of the floral correlations, and across the four field populations of black mustard, none of which showed significant differences between filament-corolla tube correla-

tions and the rest of the floral correlations. These eight populations include five source populations from three states and a variety of different growing conditions and environments (greenhouse and four different field sites in three different years; see Table 1). Second, the correlation between pistil and corolla tube was not significantly greater than the background floral correlations for any population of any species. However, four of the species were in the same family, so that the similar patterns of pistil-corolla tube correlation among these species may not be entirely independent.

The filament-corolla tube correlation patterns in three of the species (radish, canola, and phlox) are consistent with the specific hypothesis that floral correlations have been increased by selection over the background level of floral correlation to maintain proper placement of the anthers relative to the opening of the corolla tube. This hypothesis is rejected for the other two species (dame's rocket and black mustard); the filament-corolla tube correlations were not greater than the background correlation level. This does not mean that selection has not acted on correlations in these two species, only that selection has not increased the correlations between filament and corolla tube relative to the rest of the floral correlations.

The filament-corolla tube correlations are consistent with our predictions, except for phlox. In phlox and dame's rocket the anthers do not protrude beyond the opening of the corolla tube, and black mustard does not have a consistently narrow corolla tube, so we did not predict higher filament-corolla tube correlations in these species. It is not clear why phlox does not fit the prediction. It does not seem to be because the filaments are partially fused to the corolla tube, because the longest filament was highly correlated with the corolla tube, but the short filament was not ( $r = 0.71$  and  $0.36$ , respectively). Some *Phlox* species have the anthers and stigma placed outside the tubular portion of the corolla, whereas in other species they are inserted within the corolla tube as in *P. divaricata* (Grant and Grant, 1965; Levin, 1972; Levin and Berube, 1972). It would be interesting to measure the correlation patterns in additional species to see if increased filament-corolla tube correlation is found throughout the genus regardless of anther position.

While the correlation patterns in three of the species are consistent with the hypothesis of selection for effective anther placement, these results do not allow us to definitively reject the alternative hypothesis that the high correlations between the filaments and corolla tube found in these three species are caused by an ancestral developmental relationship. If this developmental hypothesis is true, however, it is clearly not true throughout the family Brassicaceae, since black mustard and dame's rocket do not show the pattern of increased filament-corolla tube correlation (Fig. 2). In fact, even within the genus *Brassica*, canola shows the pattern of increased filament-corolla tube correlation and black mustard does not. In this case the lack of phylogenetic independence among these species strengthens the case for evolutionary changes in correlation patterns, because related taxa differed. In addition, within this family the filament-corolla tube correlation patterns fit our simple predictions based on other aspects of the floral morphology (see above).

It seems clear that common developmental pathways

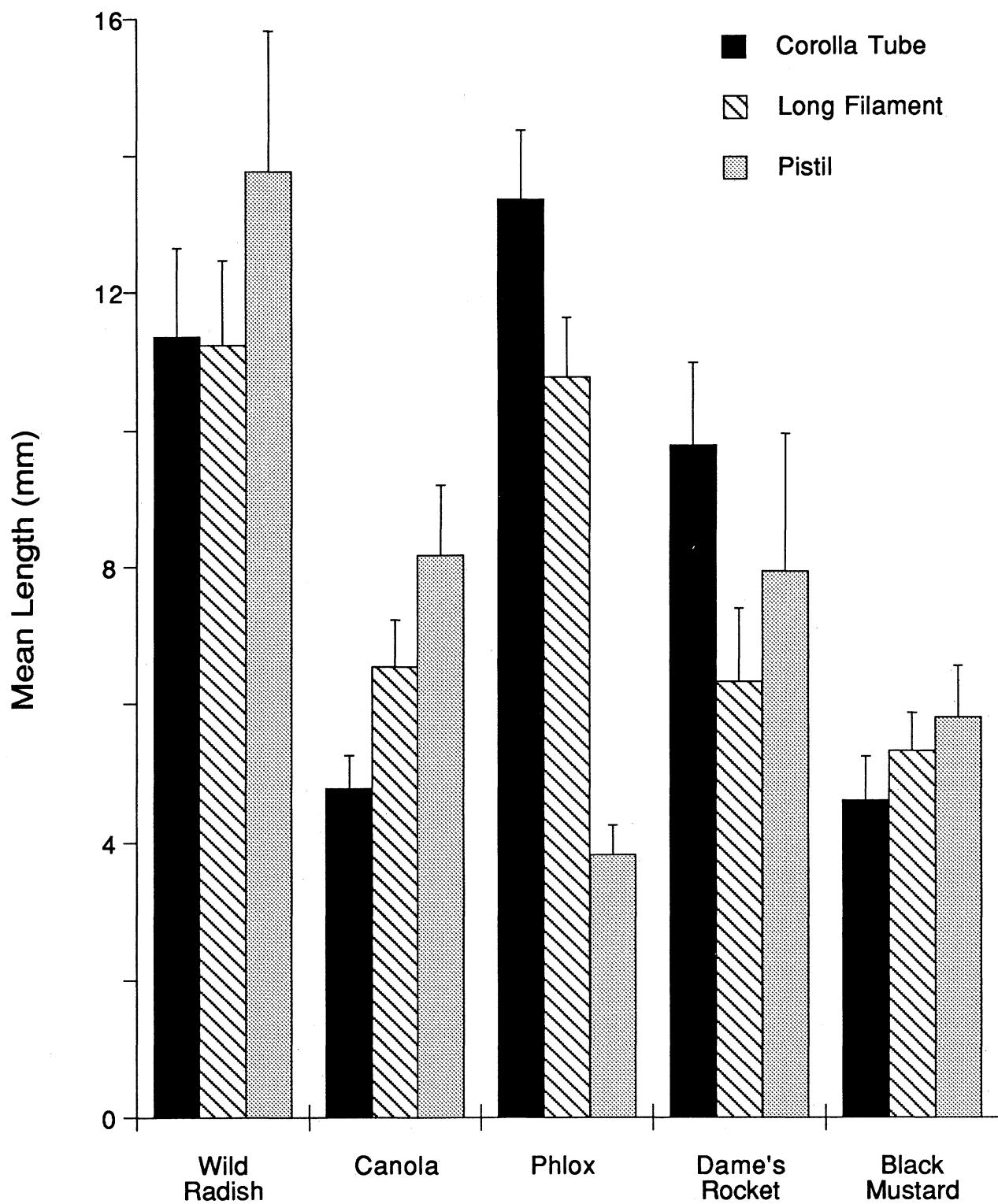


Fig. 1. Mean lengths ( $\pm 1$  SD) of the corolla tube, long filament, and pistil in the five species studied. Each group of three bars can be viewed as a schematic cross section of the flower, in which the anthers and stigma would be located at the top of the bars for filament and pistil length, respectively. There were small but significant differences among the means of the four populations of wild radish and among the four populations of black mustard studied. Within each species, however, the same patterns held in all populations so the populations are lumped here for simplicity.

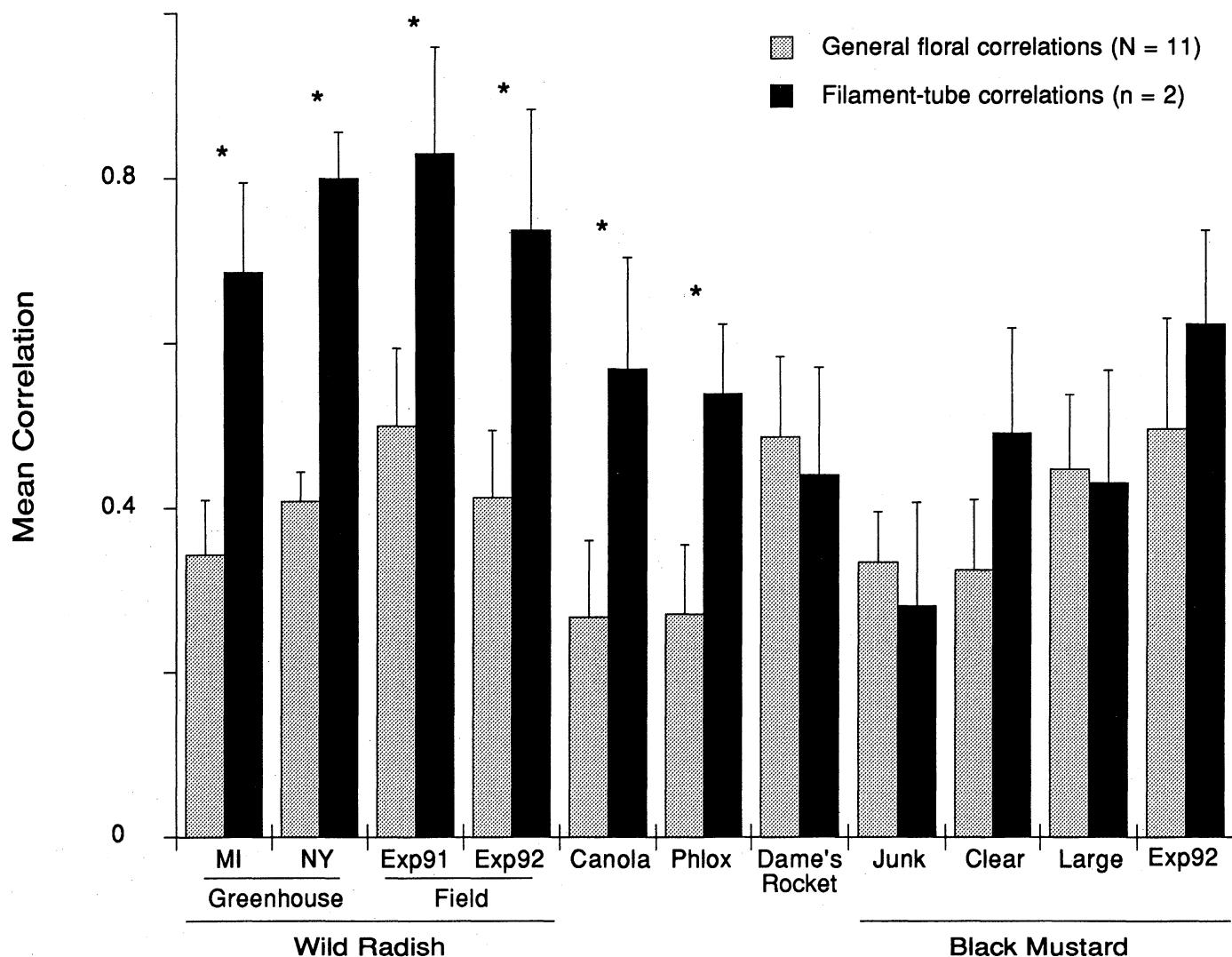


Fig. 2. Comparisons of the mean of the correlations between the two filaments and the corolla tube with the mean background level of correlation among floral traits in the 11 populations studied. Error bars are  $\pm 1$  bootstrap SD, and asterisks denote significant differences from the bootstrap.

alone cannot explain the patterns of floral correlations in these species. Note that these results do not prove that the petals and stamens are not tightly related during development in the Brassicaceae, only that these developmental relationships (if they exist) do not always lead to strong correlation between the filament and corolla tube. The increased correlation between filament and corolla tube in three of the species also cannot be explained by an hypothesis that selection has acted to maintain adequate stigma-anther separation to reduce the amount of self-pollen on the stigma (Thomson and Stratton, 1985), because this would affect the correlation between the filaments and pistil, but would not involve corolla tube lengths.

In contrast to the results for filament and corolla tube lengths, the correlation between the lengths of the pistil and corolla tube was not greater than the background level of floral correlations in any of the species. Therefore, the hypothesis that selection has increased the correlation between pistil and corolla tube lengths can be

rejected in these species. If the selection hypothesis is true for the filament-corolla tube correlation, then this result suggests that selection acts more strongly on pollen removal (male function) than pollen deposition (female function) in these flowers. Stronger selection through male function on floral traits has been demonstrated for floral color in one study (Stanton, Snow, and Handel, 1986; Stanton et al., 1989), and has been frequently postulated (Charnov, 1979; Willson and Burley, 1983; Bell, 1985; but see Wilson et al., 1994). In other words, seed set may be limited by resources rather than pollen, so that the placement of the stigma relative to the opening of the corolla tube may not be as critical to female fitness as the placement of the anthers are to male fitness (see also Harder and Barrett, 1993).

Additional studies designed to measure selection on these floral traits acting through both male and female function are needed to test further these hypotheses; we are currently pursuing these studies in wild radish and black mustard. The methods of Lande and Arnold (1983)

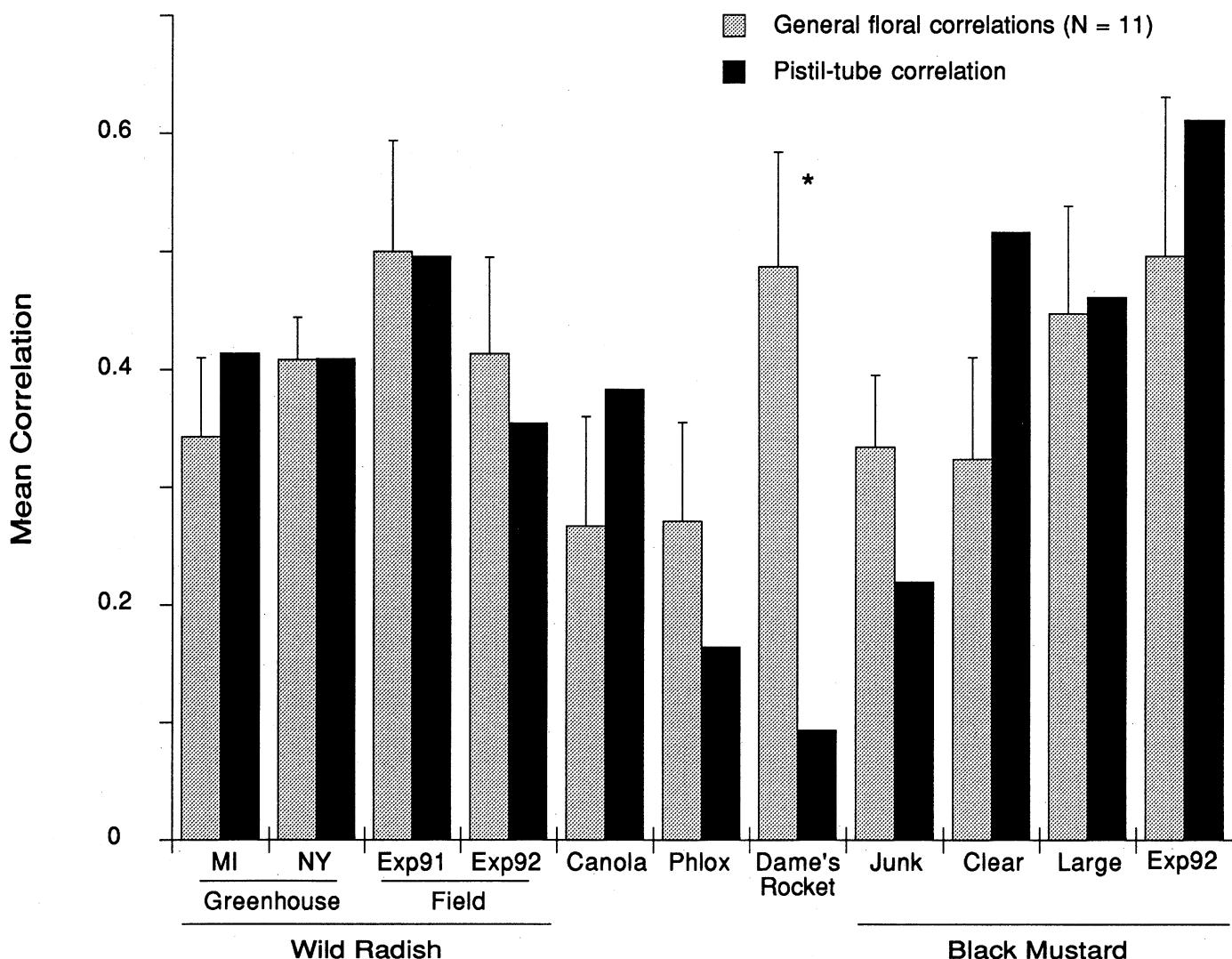


Fig. 3. Comparisons of the correlation between the pistil and the corolla tube with the mean background level of correlation among floral traits in the 11 populations studied. Error bars are  $\pm 1$  bootstrap SD, and asterisks denote significant differences from the bootstrap. The pistil-corolla tube correlation bars represent one correlation only, and therefore there are no standard errors.

are being used to test for selection on the correlations between the filaments, pistil, and corolla tube. By focusing on these two species that have similar pollinators, one of which had high correlations between the filaments and corolla tube and one that did not, we hope to gain further insight into the evolution of patterns of correlation among traits.

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