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## POLLINATOR SELECTION, QUANTITATIVE GENETICS, AND PREDICTED EVOLUTIONARY RESPONSES OF FLORAL TRAITS IN *PENSTEMON CENTRANTHIFOLIUS* (SCROPHULARIACEAE)

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Much of the remarkable diversity of angiosperm flowers is thought to have evolved in response to selection by animal pollinators. Selection during pollination can readily be documented, but the extent to which it leads to evolutionary change depends on the genetic basis of floral traits. Here we combine estimates of genetic variance and covariance for several traits of flowers and inflorescences in a wild plant species, with estimates of natural selection by hummingbird pollinators. Analysis of phenotypic selection through two components of pollination success indicates direct selection of plants toward larger size and toward bearing shorter flowers that produce more nectar. Predictions of selection response that account for genetic correlations among traits generally exceed the simple predictions based on apparent selection and heritabilities of single traits. This underscores the importance of genetic correlations and demonstrates that univariate, strictly phenotypic, analyses of natural selection can be misleading. A sample of fruits from one of the two years of our study also indicates that total selection at the end of the reproductive cycle is weaker than selection during pollination. Thus a second caution is in order, against relying too strongly on differential pollination success as an estimate of overall selection.

### Introduction

Flowers and inflorescences of higher plants are astonishingly diverse in color, fragrance, morphology, and temporal and spatial presentation (Grant and Grant 1965; Faegri and van der Pijl 1971; Proctor et al. 1996). Much of this diversity, which is central to the recognition of angiosperm species, is thought to evolve in response to selection by animal pollinators (Grant 1949; Straw 1956). The scenario for pollinator-mediated selection is as follows. Expression of flower and inflorescence traits influence that animals visit a flower, how often they visit, the efficacy of each visit in contacting sex parts, the number of other flowers visited on the same plant, and patterns of subsequent movement to other plants. In turn, these behaviors may influence the quantity and quality of pollen imported to and/or exported from a plant, and thus the plant's reproductive success as a female and/or male (Waser 1983; Stanton et al. 1986; Wyatt and Shannon 1986; Galen and Stanton 1989; Campbell et al. 1991; Devlin et al. 1992; Mitchell and Waser 1992; Hodges 1995; Andersson 1996; Connor et al. 1996).

Two conditions must be met for pollinator-mediated selection to yield an evolutionary response across plant generations. First, pollination success of individuals must correlate with final reproductive success, and indeed with total fitness (Feinsinger 1987). Second, individual variation in the expression of traits must have a genetic basis. If both these conditions are met, there

will be an evolutionary response, the trajectory of which will depend on phenotypic and genetic covariances among traits (Falconer 1989; Arnold 1992; Campbell et al. 1994; Stanton and Young 1994).

Given estimates of additive genetic variances (or heritabilities), intertrait covariances, and measures of selection, a detailed theory is available that allows quantitative predictions of the short-term trajectory of evolutionary response (Lande and Arnold 1983). In this article we describe selection on several flower and inflorescence traits in a natural plant population, as evidenced by differential attraction of pollinators and production of fruit. We then combine these measures with previously determined estimates of genetic variances and covariances. This allows us to generate predictions of evolutionary change in each of these plant reproductive traits. For each trait we compare predicted "univariate" responses that ignore phenotypic and genetic covariances of traits, with predicted "multivariate" responses that take these covariances into account. Based on this comparison, we discuss the extent to which intertrait covariances influence the predicted responses to selection.

### Material and Methods

#### The Study System

Beardtongue flowers (genus *Penstemon*; Scrophulariaceae) are diverse in morphology, color, and other traits. Different North American species attract bees, wasps, hummingbirds, and combinations of these animals as pollinators (Straw 1956; Bateman 1980; Reid et al. 1988). We studied *Penstemon centranthifolius* Benth, a short-lived California perennial, whose hermaphroditic tubular red flowers are primarily pollinated by nectar-feeding hummingbirds, with contributions from native bees and introduced honey bees (Straw 1956; Munz and Keck 1959; Mitchell 1989). Plants are self-compatible but require animal visitation to set seeds, and reproduction appears to be pollen-limited in the field

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(Mitchell 1989; R. J. Mitchell, unpublished data). Our study site was on a sandy ridge at 1450 m elevation at Summit in Cajon Pass, San Bernardino County, California, U.S.A. *Penstemon centranthifolius* blooms there from late March to early June (personal observation).

### Phenotypic Selection

We assessed pollinator responses to plant traits in 1991 and 1995. In May 1991, several pairs of observers simultaneously recorded all pollinator visits to plants in each of four semidiscrete groups of *P. centranthifolius* within the large population at the Summit study site. Each group of plants under observation consisted of 12–18 flowering individuals; in all we watched 55 plants. We observed each plant for 3 h on each of two consecutive days, for a total of 6 h per plant. In May 1995 we similarly observed three groups of 9–11 plants for 2 h on each of three nonconsecutive days, for a total of 6 h observation per plant (30 plants). Insect visits were rarely seen in either year (27 insect visits in 510 plant-hours and >18,000 flower-hours of total observation). In most cases, one male Costa's hummingbird defended a given group of plants, so our observations are based on a minimum of seven individuals, one for each group. However, intrusions by nonterritory holders were frequent. These included juvenile, female, and male Costa's (*Calypte costae*), Anna's (*Calypte anna*), and rufous hummingbirds (*Selasphorus rufus*). Thus the pollinator responses we recorded represented the activity of an estimated several tens of individual birds of both sexes of three different species.

We recorded two major aspects of pollinator visitation behavior. The first was "approaches," the number of hummingbird foraging visits to a plant per hour of observation. The second was "probes," the number of flowers that hummingbirds probed on a plant per hour of observation, divided by the number of open flowers on the plant. Combining observations from 1991 and 1995, we recorded totals of 152 approaches and 2077 probes by hummingbirds to *P. centranthifolius*.

On each plant we measured six traits of flowers and inflorescences likely to influence pollination success, defined as follows: (1) corolla length (CL) is the length of a flower measured from the base of the sepals to the opening of the corolla tube; (2) corolla width (CW) is the diameter of one of the tubular flowers at the opening; (3) pistil length (PL) is the length of the gynoecium, measured from the base of the sepals to the tip of the stigma; (4) nectar production (NPR) is the volumetric secretion of nectar by a flower in units of  $\mu\text{L}/24$  hr; (5) inflorescence height (IH) is an index of the size of the floral display, measured as distance from the base of the plant to the tip of the tallest inflorescence; and (6) total flowers (TFL) is another index of floral display, measured as the total number of open flowers on a plant averaged across the 2–3 d over which we observed that plant.

In the case of flower morphology and nectar production, we measured 1–5 flowers on each plant, and used plant means in analysis. We measured morphological traits to the nearest 0.1 mm with digital calipers. To assess nectar production, we covered buds likely to open the next day with 4 cm lengths of drinking straw, crimped at the end to prevent entry by animals (see Mitchell 1993, 1994). We returned 24 h later and measured the accumulated nectar using calibrated micropipettes. We ignore differences in nectar concentration across plants because they contribute little to individual variation in reward presented to pollinators (unpublished data).

Table 1 The G Matrix

	CL	CW	PL	NPR	IH	TFL
CL ...	<u>1.21</u> <u>0.68</u>	-0.10	0.06	1.21	-0.03	-0.29
CW ..	-0.27	<u>0.11</u> <u>0.48</u>	<u>-0.21</u>	0.21	0.00	-0.01
PL ...	0.07	<u>-0.82</u>	<u>0.60</u> <u>0.26</u>	0.44	-0.19	0.07
NPR	0.25	0.18	0.14	<u>16.00</u> <u>0.38</u>	0.02	-0.95
IH ....	-0.11	0.01	-1.0	0.02	<u>0.06</u> <u>0.40</u>	0.01
TFL	-0.48	-0.05	0.16	-0.43	0.07	<u>0.30</u> <u>0.30</u>
Mean	25.0	4.9	23.4	19.2	4.0	3.6
CV ...	5.3	8.8	6.4	38.0	6.4	26.4

Note. Estimates based on Mitchell and Shaw (1993), modified to ensure feasibility by the method of "bending" (see text). Estimates of  $V_a$  and genetic covariances are shown along and above the leading diagonal, and estimates of  $h^2$  (narrow-sense heritabilities) and genetic correlations are along and below the diagonal, in boldface. CL = corolla length (mm); CW = corolla width (mm); PL = pistil length (mm); NPR = nectar production rate (mL/24 h); IH = ln (inflorescence height in cm); TFL = ln (total flower number). Underlined values are significantly different from zero using likelihood ratio tests. Also shown are means and phenotypic coefficients of variation (CVs) for each trait from Mitchell and Shaw (1993).  $n = 137$ –179 plants for each trait.

In 1991 we also marked 10 open flowers per plant and recovered them later to estimate fruit production, one element of female reproductive success. Values of inflorescence height and total flower number were ln-transformed before analysis to improve the normality of residuals in analysis.

### Quantitative Genetics of Floral Traits

Estimates of the genetic variances and covariances for the same quantitative traits measured in the Summit field population in 1991 and 1995 (see above) are available from a previous study in another population (Mitchell and Shaw 1993). Mitchell and Shaw's methods and results can be summarized as follows: They generated paternal half-sibships by crossing one group of *P. centranthifolius* plants acting as pollen donors with a second group acting as pollen recipients. All plants were crossed in a field population near Idyllwild, California, 100 km SSW of the Summit site. The method of restricted maximum likelihood (REML; Shaw 1987; Shaw and Shaw 1992) was used to estimate additive genetic variance ( $V_a$ ), the portion of overall genetic variance available to support evolutionary change. All traits exhibited significant  $V_a$ , and equivalently significant narrow-sense heritability ( $h^2$ , table 1). Furthermore, the estimated values agree well with those obtained from another population 20 km from Idyllwild (see Mitchell and Shaw 1993). Mitchell and Shaw (1993) also calculated genetic correlations among traits using REML. These covariances were taken pairwise because an immense sample would be needed to reliably estimate all 21 variances and covariances of traits in a simultaneous analysis. The preliminary variance-covariance matrix (G matrix) assembled from these  $V_a$  and pairwise covariance values by Mitchell and Shaw (1993) was not positive definite, having a single negative eigenvalue. Therefore, we have here derived a second, feasible G matrix from the preliminary matrix by the method of "bending" (Hayes and Hill 1981). Based on the latter calculations, many traits ex-

hibited substantial genetic covariances or equivalently genetic correlations (table 1). However, large standard errors meant that only very large values were significantly different from zero.

### Predicted Response to Selection

Lande and Arnold (1983; see also Arnold and Wade 1984) showed that the vector of expected evolutionary responses ( $\Delta z$ ) to selection within a generation can be predicted as  $G\beta$ . Here  $G$  is the genetic variance-covariance matrix described above and  $\beta$  is the vector of direct selection gradients, i.e., of  $P^{-1}$ 's, obtained as unstandardized partial regression coefficients from a multiple regression of fitness on the traits in question. According to this formulation, the evolutionary change in trait  $i$  ( $\Delta z_i$ ) is the sum of the genetic change due to direct selection on that trait ( $G_{ii}\beta_i$ ) and the genetic change resulting from selection on genetically correlated traits ( $\sum_{j \neq i} G_{ij}\beta_j$ ).

As fitness components we used the two different measures of pollinator visitation rate defined above, i.e., approaches and probes. Plants receiving more approaches and more probes per flower are likely to have greater reproductive success because they receive and export more pollen (Snow and Roubik 1987; Mitchell and Waser 1992, Hodges 1995; R. J. Mitchell, unpublished data for *P. centranthifolius*). It would be ideal to have estimates of lifetime fitness for individual plants, but this is seldom practical to achieve, especially in iteroparous perennials such as *P. centranthifolius*. Because of this, and because our focus is on floral traits, we used the two different measures of pollinator visitation rate defined above as components of fitness in the analysis. Each of these focuses attention on different aspects of how pollinators affect plant reproduction (approaches indicate a plant's attractiveness at a distance, and probes indicate the number of visits received by individual flowers). Following Lande and Arnold (1983), we calculated relative fitness components by dividing approaches or probes for each plant during each day of observation by the mean for that day across all plants within the same group. We then took plant means of relative fitness components across all days of observation as response variables in multiple regressions of approaches or probes on floral traits (Lande and Arnold 1983), using PROC REG of SAS (SAS Institute 1990). In 1991 an additional fitness component was available in the form of the proportion of recovered flowers that set fruit, transformed to relative fitness as described above. Tests of selection on multiple correlated traits are not independent, but corrections to account for this are not straightforward. We therefore report conventional  $P$  values, noting that these values are anticonservative.

The response to selection was predicted from the equation  $\Delta z = G\beta$  for each of five different  $\beta$  vectors, representing approaches and probes in 1991 and 1995 and fruits in 1991. We first calculated unstandardized estimates of response, and then standardized each value by dividing it by the standard deviation (SD) of the trait ( $\Delta z'$ ; Lande and Arnold 1983). Our calculations assume that the  $G$  matrix estimated for the Idyllwild population is similar to that of the Summit population.

## Results

### Phenotypic Selection

Values of the selection differential ( $s$ ) and selection gradient ( $\beta$ ) show that hummingbirds tended to ap-

proach *Penstemon centranthifolius* plants with many open flowers in 1991. Direct phenotypic selection ( $\beta$ ) on flower number was highly significant statistically (table 2). Probes appeared to increase with nectar production and decrease with corolla length; both effects approached statistical significance. In 1995, approaches and probes both increased significantly with inflorescence height, increased somewhat less strongly with nectar production, and appeared to decrease (as in 1991) with corolla length. Proportional fruit set was positively related to nectar production and inflorescence height in 1991, but none of the relationships between flower or inflorescence traits and fruit set approached statistical significance.

These results indicate a strong response of hummingbirds to plants with larger floral displays, and a weaker but consistent response in favor of greater nectar production and against longer flowers. The fact that the regression analysis identifies flower number as a target of selection in 1991 but switches to inflorescence height as a target in 1995 should not necessarily be taken to mean that hummingbirds actually responded to different aspects of floral display size in different years. We say this because the phenotypic correlation between these traits was strongly positive, especially in 1995 (1991:  $r = 0.27$ ; 1995:  $r = 0.90$ ). When two independent variables are correlated in this way, which trait is assigned a large partial regression coefficient may be determined by minor differences in the data structure (Mitchell-Olds and Shaw 1987). The negative coefficients for flower number in 1995 probably result from such instability and are not biologically meaningful. A positive simple correlation between probes and flower number ( $r = 0.25$ ;  $P = 0.17$ ) in 1995 is consistent with this interpretation.

### Predicted Response to Selection

We can multiply the estimated heritabilities of individual traits ( $h^2$ ; table 1) by observed overall selection on those traits ( $s$ ) to predict an evolutionary response in the value of each trait (Falconer 1989; Galen 1996). This univariate analysis predicts evolutionary change toward plants that produce more flowers with more nectar and perhaps shorter flowers as well (table 2).

These univariate predictions are likely to be misleading, however, because they ignore the contributions to selection response of a particular trait that are due to change in traits that are genetically correlated with that trait. Multivariate analyses are required to account for such genetic correlations. For example, the univariate predictions were for modest increases in nectar production as a response to approaches and probes in both years, whereas the multivariate predictions for  $\Delta z$  were larger for 4 of 5 measures, by factors ranging from 1.4 to 4 (table 2). Similarly, the univariate prediction was for a small evolutionary increase in plant height, whereas the multivariate prediction tended to be about twice as great. In other cases, strong genetic correlations (table 1) apparently were respon-

Table 2 Selection and Predicted Response

	Trait	<i>s</i> ( <i>P</i> )	$\beta$ ( <i>P</i> )	<i>h</i> <sup>2</sup> <i>s</i>	$\Delta z_i$	$\Delta z_i'$
1991 approaches .....	CL	-0.04 (0.82)	-0.06 (0.52)	-0.03	-0.16	-0.12
	CW	-0.02 (0.74)	-0.04 (0.85)	0.01	0.00	0.00
	PL	-0.17 (0.37)	0.01 (0.95)	-0.04	0.05	0.03
	NPR	0.64 (0.32)	0.03 (0.19)	0.24	-0.07	-0.01
	IH	0.02 (0.30)	0.01 (0.99)	0.01	0.01	0.04
	TFL	<b>0.57 (0.0001)</b>	<b>0.48 (0.001)</b>	0.17	0.14	0.12
1991 probes .....	CL	-0.28 (0.13)	-0.17 (0.13)	-0.19	-0.22	-0.16
	CW	0.02 (0.74)	0.23 (0.45)	0.01	0.06	0.11
	PL	-0.25 (0.26)	-0.01 (0.92)	-0.06	-0.12	-0.07
	NPR	0.89 (0.21)	0.04 (0.13)	0.33	0.45	0.09
	IH	0.02 (0.29)	0.39 (0.66)	0.01	0.03	0.18
	TFL	0.15 (0.32)	0.11 (0.41)	0.04	0.04	0.04
1991 fruits .....	CL	0.22 (0.12)	0.11 (0.21)	0.15	0.12	0.09
	CW	0.06 (0.24)	0.22 (0.35)	0.03	0.02	0.03
	PL	0.12 (0.48)	0.01 (0.94)	0.03	-0.16	-0.10
	NPR	0.30 (0.58)	0.02 (0.51)	0.11	0.45	0.09
	IH	0.02 (0.35)	0.65 (0.34)	0.01	0.03	0.21
	TFL	0.02 (0.86)	-0.03 (0.76)	0.01	-0.05	-0.05
1995 approaches .....	CL	-0.06 (0.69)	-0.05 (0.55)	-0.04	-0.02	-0.02
	CW	0.01 (0.81)	0.13 (0.52)	0.00	0.02	0.05
	PL	-0.27 (0.14)	0.03 (0.64)	-0.07	-0.28	-0.16
	NPR	<b>0.95 (0.028)</b>	0.04 (0.09)	0.36	0.77	0.18
	IH	<b>0.11 (0.0008)</b>	<b>1.40 (0.047)</b>	0.04	0.08	0.24
	TFL	<b>0.32 (0.011)</b>	-0.12 (0.47)	0.10	-0.05	-0.04
1995 probes .....	CL	-0.13 (0.67)	-0.21 (0.22)	-0.09	-0.07	-0.05
	CW	0.04 (0.70)	0.31 (0.49)	0.01	0.05	0.11
	PL	-0.29 (0.46)	0.17 (0.22)	-0.07	-0.68	-0.39
	NPR	<b>2.15 (0.018)</b>	<b>0.11 (0.041)</b>	0.81	2.23	0.53
	IH	<b>0.16 (0.024)</b>	<b>3.59 (0.022)</b>	0.06	0.20	0.62
	TFL	0.38 (0.17)	-0.60 (0.12)	0.11	-0.18	-0.15

Note. Selection estimates (selection differential *s*; selection gradient  $\beta$ ; and their associated *P*-values) and predicted univariate (*h*<sup>2</sup>*s*) and multivariate responses to selection. Two versions of the multivariate response are given: the first ( $\Delta z_i$ ) is in the units of measurement for the trait; the second ( $\Delta z_i'$ ) is standardized and is in units of phenotypic standard deviations (SD) of the trait. For 1991 data, *n* = 55 plants; for 1995, *n* = 30. For *s* and  $\beta$ , statistically significant values are shown boldface. For explanation of abbreviations, see table 1.

sible for multivariate predictions in a direction opposite to univariate predictions. For example, a positive genetic correlation of total flower number with pistil length, and a negative correlation of pistil length with inflorescence height, translated the positive univariate prediction for flower number into a negative multivariate prediction in 1995. Overall, multivariate predictions tended to be larger than univariate predictions, indicating that phenotypic and genetic correlations may enhance evolutionary change in this system.

The predictions just discussed derive from pollinator behavior. Predictions from proportional fruit maturation are for no substantial evolutionary change in any floral or inflorescence trait measured, except perhaps nectar production and inflorescence height (table 2).

### Discussion

Our results indicate that quantitative variation in floral traits can strongly influence components of fitness and that some of these effects can remain qualitatively similar across years and fitness components, while differing in magnitude (see also Campbell 1989, 1991). They also serve as a reminder that substantial knowledge of genetics, including genetic correlations among traits, is needed before one attempts to predict evolutionary responses from phenotypic selection measures

(Falconer 1989; Grant and Grant 1993, 1995, Galen 1996). The specific predictions of evolutionary change in *Penstemon centranthifolius* may help shed light on the evolution of diversity in floral trait expression more generally.

### Phenotypic Selection

The most consistent result was that hummingbirds favored plants that presented more food reward, as measured by the nectar production of flowers. This effect was consistent between years and is unsurprising given that hummingbirds and other pollinators respond strongly to rewards when choosing flowers (e.g., Waser 1983; Mitchell 1993; Hodges 1995; Meléndez-Ackerman et al. 1997). A comparison of estimates of *s*, which were large, and of  $\beta$ , which were small (table 2) shows, however, that much of this selection on nectar production was indirect. This indirect selection results from phenotypic correlations of nectar production with other floral traits (presented in Mitchell and Shaw 1993. These correlations range from 0.03 to 0.14; the highest value is the correlation with inflorescence height.) The size of a plant's floral display, especially assessed as inflorescence height, also had a strong positive effect on pollinator visitation. This was true even though we assessed visitation (probes/flower/hour) on

a per-flower, rather than per-plant, basis (contrast Klinkhamer et al. 1989; Herrera 1991; Muenchow and Delesalle 1994). Thus, each increment in floral display increased total visitation rate, which is likely to increase total reproductive success, especially for self-compatible plants such as *P. centranthifolius* (see Klinkhamer and de Jong 1993).

Effects of flower size and shape on hummingbird visitation were relatively weak. Only corolla length appeared to be related consistently, albeit weakly, with pollination. These results indicate that hummingbirds may respond more to the inflorescence or plant as a unit of attraction than to individual flowers. In contrast, the accepted "syndrome" of floral traits related to hummingbird pollination (Grant and Grant 1968; Proctor et al. 1996) implies that individual flower size and shape strongly determine pollination success (see also Temeles 1996). Interestingly, flowers with long corolla tubes are classically considered an important part of the hummingbird syndrome, yet birds showed reasonably strong preferences for *shorter* corolla tubes ( $\beta$  values ranging from  $-0.06$  to  $-0.21$ ; table 2).

Although we detected fairly consistent selection involving hummingbird visitation, we could detect much less at the level of fruit production. One reason may be that our assessment of fruit production was more limited than that for visitation, being restricted to a single year and to ten flowers per plant. On the other hand, pollinator visitation need not necessarily translate into detectable differences in female fitness (i.e., seed set and fruit set) in all years (Burd 1994). Indeed, the correlations between fruit set and visitation rate were near zero (for approach rate,  $r = 0.004$ , and for probes/flower,  $r = -0.020$ ).

#### Predicted Response to Selection

Even strong selection need not result in a large predicted evolutionary response, as results for floral display size in *P. centranthifolius* show. The reason lies in the structure of genetic variance of traits and, hence, their heritability, which usually is well below unity, and of intertrait covariance, which further modifies evolutionary response. Because genetic covariances for wild plant species may often be substantial (Mitchell-Olds 1986; Mitchell and Shaw 1993; Campbell et al. 1994; Young et al. 1994; Shaw et al. 1995; Andersson 1996; Campbell 1996; Galen 1996), we infer that imperfect relationships between selection and response and between univariate and multivariate predictions of response are the norm. The nature of these relationships bears further empirical study in the tradition of Johnston (1991), Grant and Grant (1993, 1995), Campbell et al. (1994), Stanton and Young (1994), Andersson (1996), Campbell (1996), and Galen (1996).

Understanding the details of genetic variance and covariance is likely to change interpretation of the widespread evidence for strong phenotypic selection on floral traits (Waser and Price 1983; Stanton et al.

1986; Campbell 1989; Galen 1989; Cresswell and Galen 1991; Johnston 1991; Devlin et al. 1992; Mitchell 1993; Hodges 1995). Until heritabilities and genetic correlations are known, or multigeneration selection experiments determine whether responses are modified by correlations (see Stanton and Young 1994), we cannot interpret evidence of phenotypic selection within a single generation (which yields estimates of  $s$  and/or  $\beta$ ) as an indication of the magnitude, or even sign, of expected short-term evolutionary change, no matter how tempting it is to do so.

Understanding genetic variance-covariance structure is also likely to be critical for explaining the existence of genetic variation for traits that appear to be related directly to components of fitness such as nectar production or floral display size. It seems enigmatic that natural populations harbor substantial variation in such traits, as they indeed do (e.g., Campbell 1989, 1991, 1996). However, this apparent enigma is removed if fitness components have strong negative genetic covariances with one another (Barton and Turelli 1989), though we found few instances of such trade-offs in our data (table 1).

Finally, appreciating the constraints imposed by genetic covariances raises questions about the evolution of apparently specialized pollination syndromes (e.g., red tubular corollas and high nectar production rates for hummingbird-pollinated plants). If covariances are large, selection on each of many independent traits making up a syndrome seems unlikely to generate an exact fit between plant and pollinator. Yet the very existence of syndromes apparently belies this argument. Perhaps, in contrast to the more traditional view, the traits associated with the floral syndromes do not evolve independently, and instead only a few constellations of traits that may be genetically correlated (Conner and Via 1993) have evolved in directions that promote pollination by particular animals. Additionally, the "fit" of plant and pollinator may be less exact than sometimes suggested (Wilson 1995; Armbruster 1996; Waser et al. 1996). More information on genetic correlations among floral traits for wild plant populations is needed to test these hypotheses, as is information about behavioral responses of animals to the plants they pollinate.

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