

Selection on Floral Morphology by Hummingbirds

Darwin (1859) recognized that pollinators may be important selective agents in the evolution of floral morphology. For instance, he believed that the extremely long corolla tubes or nectar spurs of some orchids were the result of directional selection by long-tongued pollinators (Darwin 1862). Nilsson (1988) confirmed Darwin's hypothesis by demonstrating that experimental shortening of floral tubes was associated with a decrease in pollinia removal and receipt in the hawkmoth-pollinated orchids *Platanthera bifolia* and *P. chlorantha*. In addition, longer-spurred *P. bifolia* in a natural population had greater rates of fruit production. Moths visiting longer-spurred orchids are forced to drive their proboscises deeper into the flower and therefore act as legitimate pollinators rather than nectar thieves. His data are strong evidence for the presence of directional selection on orchid spur length by hawkmoth pollinators.

Species with long corolla tubes are often associated with low pollinator diversity and are thought to have evolved in response to selection by long-tongued or long-billed pollinators (Darwin 1862; Grant & Grant 1965; Nilsson *et al.* 1985, 1987; Nilsson and Rabakonandrianina 1988). Long corolla tubes allow species to conceal their nectar from generalist pollinators (Proctor & Yeo 1973). Within the general syndrome of hummingbird pollination, taxa with shorter corollas are often not exclusively hummingbird-pollinated (Grant & Grant 1968). In a neotropical highland community, species with long corollas are associated with a lower diversity of hummingbird pollinators compared to species with shorter corollas (Wolf *et al.* 1976). However, pollinators visiting long-corolla flowers do not usually specialize on only one species. This has been observed for taxa pollinated by hawkmoths (Kislev *et al.* 1972, Nilsson *et al.* 1987) and hummingbirds (Feinsinger *et al.* 1986). Pollen transfer to conspecifics in long-corolla species may be enhanced by species-specific placement of pollen on the body of the pollinator. In contrast, short-corolla flowers do not show the same specificity of pollen transfer (Feinsinger 1983, Feinsinger *et al.* 1986, Nilsson *et al.* 1987).

The observed low pollinator diversity and specificity of pollen placement associated with increasing corolla length suggests that the strength of stabilizing and/or directional selection on corolla tube length is greater for species with long corollas than for those with short corollas. A trait under long-term directional or stabilizing selection will experience a reduction in genetic variation which may result in a reduction of phenotypic variation (Fisher 1958, Lande & Arnold 1983). Long-term directional selection may also result in a trait coming under opposing forces of natural selection leading to a net effect of stabilizing selection (Falconer 1981). If species with long corollas experience greater stabilizing or directional selection on corolla length, then the phenotypic variance of corolla length may be reduced compared to species with shorter corollas. Few studies have documented the selective forces determining flower morphology (Endler 1986). Here I use the great diversity of hummingbirds and hummingbird-pollinated taxa in the neotropics to test the prediction that variance in corolla length is negatively correlated with mean corolla length using comparisons between species.

Corolla lengths of hummingbird-pollinated flowers were measured at three field sites in Costa Rica in February and March 1984: Monteverde (Mont), a low montane forest (1200–1800 m); Cerro de la Muerte (CdM), a tropical highland community (3000 m); and La Selva (LSel), a lowland (29–100 m) evergreen forest (Hartshorn 1983). Corolla length was measured (to the nearest 0.1 mm using calipers) as the length from the base of the petals to the most distal part of the flower that would allow the pollinator entrance to the corolla tube. The following *a priori* method for choosing species for comparisons was used. The increase of variance in corolla length with increasing sample size was determined for each species at each site. If the increase in variance displayed a plateau, the species was included in the analysis. Corolla length variation usually stabilized when 10 or more individuals were sampled from a population. This method resulted in a total of 10 species suitable for the comparisons: six from Mont (of 12 sampled), and two each from CdM and LSel (Table 1). The larger number of species sampled at Mont reflect greater sampling time. Heteroscedasticity of variances often arises through a positive correlation of variance with the mean (Wright 1968) and was observed in this study. To determine the intrinsic variation of corolla length, *i.e.*, the variation independent of the mean, the raw data (mean corolla length per individual) were ln-transformed (Lewontin 1966) before the variance for each species was calculated.

Corolla length variation was documented by pooling flowers across individuals and by determining the amount of corolla length variation among individuals. The first method inflates the contribution of environmental sources of variation but includes a measure of developmental canalization of corolla tube

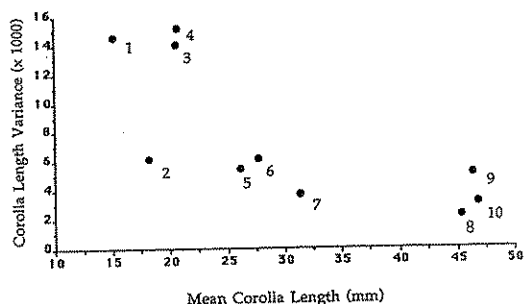


FIGURE 1. Relationship between corolla length and variance of ln-transformed corolla length for 10 neotropical hummingbird-pollinated species. Flowers were pooled across all individuals within a species. Numbers to side of dots refer to species listed in Table 1. Note values on ordinate are multiplied by 1000.

length. In contrast, the amount of variation in corolla tube length among individuals is an upper estimate of the amount of genetic variation for this trait. If stabilizing selection on floral characters is more important in long-corolla species then both variation among and within individuals should be reduced. Since so few flowers of *Centropogon solanifolius* were sampled per individual, this species was not included in the analysis of variation among individuals.

As predicted, there is a negative correlation between corolla length and variance in ln-transformed corolla length among the 10 species (Fig. 1, Spearman rank correlation for analysis pooling flowers across individuals = -0.84 , 8 df, $P < 0.005$, Spearman rank correlation for variation among individuals = -0.68 , 7 df, $P < 0.05$). This negative association is also observed in comparisons among species with very different corolla length within the same family (Acanthaceae, $F = 2.7$, $P < 0.001$) and among species within the same genus (*Centropogon*, $F = 1.74$, $P < 0.05$) (Fig. 1 and Table 1). Therefore, the relationship between corolla length and variance in corolla length appears to be independent of any phylogenetic constraints. One might expect greater developmental variation in species with longer corollas, since longer corollas may take longer to develop and thus be exposed to greater environmental influence (Stebbins 1950). However, no relationship was observed between the proportion of variation of corolla length within individuals and corolla length among the 10 species (Spearman rank correlation = 0.26 , 8 df, NS). Perhaps this lack of association reflects greater developmental canalization in long-corolla species experiencing stabilizing selection which nullifies exposure to greater environmental sources of variation.

The observed variation in corolla length for some taxa probably reflects processes other than increasing pollinator specialization and greater selective pressures with increasing corolla length. For example, *Cephaelis elata* (sp. #1, Table 1, Fig. 1) has a short corolla and a relatively large variance of corolla length. However, it is heterostylous (suggesting strong selection for precise dimensional relationships between the characters involved in the pollination process), it is pollinated predominantly by one hummingbird species *Lampornis calolaema* (Feinsinger *et al.* 1988), and it is in pollinator competition with *Palicourea lasiorachis*, which may exert selective pressures on corolla traits (Feinsinger *et al.* 1988). These conditions suggest that corolla morphology should be under intense selection. In contrast, *Lobelia laxiflora* (sp. #7, Table 1, Fig. 1) is a relatively long-corolla species, with decreased corolla length variance. Because of high flower density and local abundance of nectar resources, the aggressive behavior of territorial hummingbirds is diminished and *L. laxiflora* is visited by a number of hummingbird species of various bill lengths (Feinsinger 1976). If these species are all pollinators, then *L. laxiflora* should not be considered as possessing a specialized pollinator guild. The amount of corolla length variation in a population may reflect the extent to which the trait is environmentally determined or may reflect historical processes, *e.g.*, previous selection episodes or inbreeding due to population bottlenecks. The comparative approach used here also reveals anomalous relationships. For example, the relatively low variation observed in the short-corolla *C. crassifolia* (sp. #2) suggests this species is specialized in some way other than corolla length. There are a number of instances where the data correspond to the ecology of the species. *Hamelia patens*

TABLE 1. Sampling regime and summary statistics of hummingbird-pollinated plants. Plants are listed in order of increasing corolla length (CL).

Species	Family	Site	No. of plants	Mean no. of flowers per individual	Mean CL (mm)	CL $\sigma^2 \times 1000$ (ln)	CL $\sigma^2 \times 1000$ (ln)
1. <i>Cephaelis elata</i>	Rubiaceae	Mont	17	4.1	15.2	14.5	10.7
2. <i>Cavendishia crassifolia</i>	Ericaceae	Mont	17	4.4	18.2	6.1	3.2
3. <i>Hansteinia blepharorachis</i>	Acanthaceae	Mont	20	3.3	20.7	14.0	17.1
4. <i>Hamelia patens</i>	Rubiaceae	LSel	15	4.9	20.8	15.1	12.5
5. <i>Centropogon costaricense</i>	Lobeliaceae	CdlM	13	4.5	26.2	5.4	4.4
6. <i>Bomeria acutifolia</i>	Arnyllidaceae	CdlM	13	5.0	27.8	6.1	5.4
7. <i>Lobelia laxiflora</i>	Lobeliaceae	Mont	23	4.9	31.3	3.7	2.8
8. <i>Heliconia</i> sp.	Musaceae	LSel	15	3.9	45.4	2.2	1.1
9. <i>Razisea spicata</i>	Acanthaceae	Mont	21	4.9	46.4	5.1	3.2
10. <i>Centropogon solanifolius</i>	Lobeliaceae	Mont	16	1.7	46.8	3.1	3.5

(sp. #4, Table 1, Fig. 1), a short-corolla species, is pollinated by both insects and hummingbirds (Feinsinger 1976) and has a relatively high variance, as might be expected for a species pollinated by a variety of pollen vectors. Two species with long corollas and low variance, *Heliconia* sp. (sp. #8, Table 1, Fig. 1) and *Centropogon solanifolius* (sp. #10, Table 1, Fig. 1), are visited by hermit hummingbirds, whose beak morphologies are often more closely adapted to flower shape than those of other hummingbirds (Snow & Snow 1972).

Lower variation in corolla tube length in long-corolla species may not be due to selection on corolla length itself. A reduction in variance in corolla tube length could occur if it is correlated with another trait that is the target of selection (Lande & Arnold 1983), e.g., corolla tube width. In addition, increasing floral specialization due to competition for pollinators could occur through a variety of mechanisms, aside from increasing corolla length. For example, pollinator specificity can evolve through evolution of fragrances (van der Pijl & Dodson 1966, Nilsson 1983, Nilsson *et al.* 1985), color (Grant & Grant 1968), nectar production (Wolf *et al.* 1976), phenology (Feinsinger 1983), and other morphological features of the corolla (Faegri and van der Pijl 1979; Nilsson 1983; Nilsson *et al.* 1987). Pollinator specificity may also be determined by interactions among pollinators (Feinsinger 1976). Only studies within populations which document the selective forces on floral trait variation will reveal the processes by which corolla size has evolved (e.g., Nilsson 1988, Campbell 1989, Schemske & Horvitz 1989). The present survey of ten hummingbird-pollinated species suggests that hummingbirds exert strong selective pressures on corolla morphology across several neotropical plant communities.

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