



Functional Significance of Interspecific Variation in *Burmeistera* Flower Morphology: Evidence from Nectar Bat Captures in Ecuador

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ABSTRACT

What causes flowers to diverge? While a plant's primary pollinator should strongly influence floral phenotype, selective pressures may also be exerted by other flower visitors or competition with other plants for pollination. Species of the primarily bat-pollinated genus *Burmeistera* (Campanulaceae) frequently cooccur, with up to four species in a given site, and broadly overlap in flowering phenology, typically flowering throughout the year. The genus displays extensive interspecific variation in floral morphology in the degree that the reproductive parts (anthers and stigma) are exerted outside of the corolla, and species can be roughly classified as either long or short-exserted. I tested two hypotheses regarding the functional significance of such variation: (1) exertion lengths correspond to pollination by bat species of different sizes; and (2) variation serves to partition pollinator's bodies spatially and thus reduces interspecific pollen transfer. I captured bats in Ecuador to evaluate the identity and location of the *Burmeistera* pollen they were carrying. Results show that exertion does not correspond to specialization on different pollinators; different bat species carried pollen of both flower types just as frequently. In support of the second hypothesis, pollen from flowers of different exertion lengths was found to occur on different regions of bats' heads. This may serve to reduce competition for pollination among coexisting *Burmeistera*.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: Campanulaceae; floral morphology; hummingbird; Neotropics; pollination; specialization.

WHAT CAUSES FLOWERS TO DIVERGE? Biologists have long been intrigued by the extensive variation in floral morphology across angiosperms (Darwin 1862, Grant 1949). Pollinators impose strong selective pressures on floral form (Campbell *et al.* 1996, Cresswell 2000, Alexandersson & Johnson 2002); however, their role in floral divergence is not always obvious. Although the 'fit' between a flower and its most effective pollinator is important (Stebbins 1970, Armbruster *et al.* 2004, Muchhala 2007), floral morphology may also evolve to either facilitate or exclude less-effective pollinators (Aigner 2001). Competition for pollination can also select for floral divergence to reduce fitness costs associated with interspecific pollen flow (Rathcke 1983, Waser 1983, Armbruster 2006).

The speciose Neotropical genus *Burmeistera* (Campanulaceae) displays high interspecific variation in flower morphology in the length of the staminal column (Muchhala 2006a). The genus is primarily bat-pollinated, with occasional secondary pollination by hummingbirds; only one species (*B. rubrosepala* (E. Wimm) E. Wimm) is known to have adapted exclusively to hummingbird pollination (Muchhala & Jarrin-V. 2002; Muchhala 2003, 2006a). Flowers are protandrous, and the length of the staminal column determines the degree of exertion of the anthers and stigma outside of the corolla opening. For nine bat-pollinated species, the degree of exertion of the reproductive parts varies from 11.6 to 27.3 mm (coefficient of variation: 0.33), while other corolla measurements show remarkably little variation (coefficient of variation for inner width: 0.09; outer width: 0.14; greater length: 0.15; lesser length: 0.15; Muchhala 2006a). When data are included for 12 other *Burmeistera*, the frequency of exertion lengths displays a bimodal distribution, with one peak at 16 mm and another at 24 mm

(Fig. 1). Thus, flowers can be roughly categorized as long-exserted or short-exserted (hereafter I will also refer to these as 'long' or 'short').

What selective pressures may have been responsible for this bimodal distribution of floral morphology across *Burmeistera*? Previous work in Costa Rica found that a long-exserted species (*B. cyclostigmata* Donn. Sm.) was visited by both bats and hummingbirds yet only pollinated by bats, while a short-exserted species (*B. tenuiflora* Donn. Sm.) was pollinated primarily by bats and secondarily by hummingbirds (Muchhala 2003). This suggests that short-exsertion may serve to increase stigma and another contact with hummingbird visitors, and thus may represent an adaptation to facilitate generalization on both bats and hummingbirds. However, more recent work in Ecuador (Muchhala 2006a) failed to support this hypothesis; for the nine species of *Burmeistera* studied, the present hummingbird contribution to the total pollen that flowers received was similar for long-exserted species (mean: 5.5%; range: 2.2–8.9%, $N = 3$) and short-exserted species (mean: 5.4%; range: 1.6–16.0%, $N = 6$). For both types of flowers, bats contributed nearly 95 percent of pollen transfer on average. Furthermore, the only known species of *Burmeistera* that is exclusively hummingbird-pollinated (*B. rubrosepala*) is actually long-exserted, rather than short-exserted as this hypothesis would predict (Muchhala 2006a).

In this study, I captured bats and analyzed pollen loads of *Burmeistera* species to evaluate two additional hypotheses regarding the adaptive significance of the observed variation in exertion length. The first proposes that differences in exertion correspond to size differences in the pollinator species. Over much of the range of *Burmeistera* in Ecuador, two species of nectar bats (Phyllostomidae: Glossophaginae) occur sympatrically (Koopman 1981). One (*Anoura geoffroyi* Gray) is larger than the other (*A. caudifer* (E. Geoffroy)) by approximately 20 percent, with a mean skull length of

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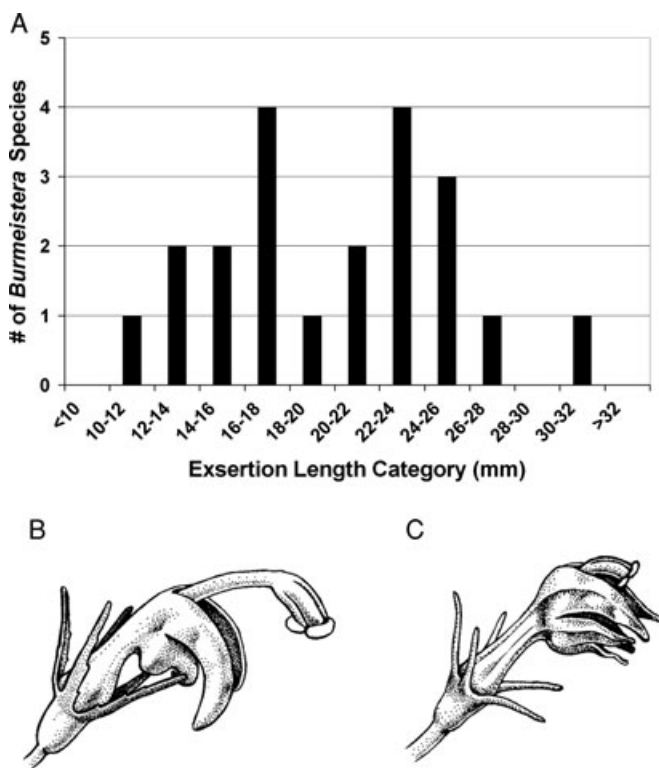


FIGURE 1. Exsertion length of *Burmeistera* floral reproductive parts. (A) Frequency distribution of exsertion length for 21 species of *Burmeistera*. Exsertion length was measured from fresh specimens as the distance (mm) from the constricted part of the corolla tube to the distal tip of the anther tube. (B) Example of a long-exserted flower (*B. truncata*; reprinted from Muchhala & Jarrin 2002). (C) Example of a short-exserted flower (*B. succulenta*).

25.7 versus 21.8 mm (Muchhala *et al.* 2005). Larger skulls may select for longer exsertion in *Burmeistera* flowers to best 'fit' the bats' head and thus to maximize pollen transfer. This hypothesis predicts that pollen from long *Burmeistera* species will be more common on large bats (*A. geoffroyi*), and pollen from short *Burmeistera* on small bats (*A. caudifer*).

The second hypothesis proposes that the difference in exsertion serves to reduce competition for pollination by spatially partitioning bats' bodies. Thirty-six species of *Burmeistera* are known to occur in Ecuador (Lammers 2007), and two to four species cooccur in any given cloud forest. For sympatric plants, sharing a pollinator can lead to high rates of interspecific pollen transfer, which may negatively affect fitness by causing stigmas to be clogged by foreign pollen (Waser 1978, Armbruster & Herzig 1984, Caruso & Alfaro 2000, Brown & Mitchell 2001) and by causing pollen to be lost to foreign stigmas (Campbell & Motten 1985). Divergence of pollen placement can reduce such costs (Howell 1977, Brown & Kodric-Brown 1979, Armbruster *et al.* 1994). While multiple lines of evidence are needed to fully test this hypothesis, one critical prediction I examine here is that pollen from long and short species will be placed on different regions of bats' heads.

METHODS

STUDY SYSTEM.—The Neotropical genus *Burmeistera* (Campanulaceae) comprises 102 species distributed from Guatemala to Peru, reaching its highest diversity in the cloud forests of the Andes (Lammers 2007). Thirty-six species occur in Ecuador, with up to four species cooccurring at any given site (Muchhala 2006a). Flowers of the genus are zygomorphic (bilaterally symmetrical) with tubular corollas. Long pedicels place flowers beyond the foliage, at approximately 45° above the horizon. A staminal column positions reproductive parts above the corolla opening; the length of this column determines the degree of exsertion of the reproductive parts. Anthers are fused together to form a tube into which pollen is shed. Flowers are protandrous; during the male-phase, pollen is released gradually through the open end of this tube via a 'pump mechanism' as the style elongates within the tube (Erbar & Leins 1995). When the stigma emerges from the tube, its dorsal and ventral lobes open and the female-phase begins. Sympatric species overlap in flowering time. Flowers remain open for several days, plants flower for several months, and populations remain in flower throughout the year (with somewhat lower flowering levels during the dry season; N. Muchhala, pers. obs.).

Fieldwork was conducted in the Yanayacu and SierrAzul reserves on the eastern slopes of the Andes of Ecuador and the Bellavista and Golondrinas reserves on the western slopes, during eight field trips from April 2003 through September 2004 (Table 1). Ten species of *Burmeistera* occur at these sites in total, with three to four species cooccurring in each (Table 1). Four of these ten species are short-exserted and five are long-exserted. The remaining species (*B. sodiroana* Zahlbr.) is 'short' (15.8 mm) on the eastern slopes of the Andes (Yanayacu) and 'long' (20.1 mm) on the western slopes (Bellavista).

Three species of nectarivorous bats occur in these cloud forest sites: *Anoura geoffroyi*, *A. caudifer*, and *A. fistulata* (Muchhala, Mena, & Albuja). Of these, only the first two were found to visit *Burmeistera*; the extremely long-tongued *A. fistulata* was never found carrying the pollen of this genus (Muchhala *et al.* 2005). *Anoura geoffroyi* is approximately 20 percent larger than *A. caudifer* by various measures (*e.g.*, skull, body, and forearm length; Muchhala *et al.* 2005).

BAT CAPTURES.—Bats were captured with mist nets set at ground level. Where possible, these were placed in front of *Burmeistera* or other known bat-pollinated plants. I typically set ten nets each night (three 12 × 3 m, three 6 × 3 m, and four 3 × 3 m). These were opened from 1800 to 0000 h and checked every half hour. Over the 70 d of fieldwork, this represents approximately 4200 net hours in total. Insectivorous and frugivorous bats were identified and released. Before removing *Anoura* from the mist nets, I collected pollen from their fur with a strip of clear tape that I then placed on a microscope slide. As I placed the tape along the top of the head, I marked the position of the noseleaf (with a vertical line) and the direction of the head (with an arrow). When I analyzed these samples with a light microscope, this allowed me to count all pollen grains occurring in three separate regions: 0–7 mm from the

TABLE 1. List of study sites with locations, elevations, and *Burmeistera* species present. For each species, the exertion type is given (L = long-exserted; S = short-exserted) as well as the exertion length in millimeters.

Reserve	Province	Location	Elev. (m)	<i>Burmeistera</i> Present (Exsertion Type; mm)
Bellavista	Pichincha	00°01' S, 78°41' W	2000–2400	<i>B. cylindrocarpa</i> (S; 14.2), <i>B. sodiroana</i> (L; 20.1), <i>B. succulenta</i> (S; 11.3)
Golondrinas	Carchi	00°50' N, 78°07' W	1600–2400	<i>B. cyclostigmata</i> (L; 28.6), <i>B. lutosa</i> (S; 11.8), <i>B. holm-neilsenii</i> (L; 19.7), <i>B. multiflora</i> (S; 16.7)
SierrAzul	Napo	00°38' S, 77°55' W	2200–2800	<i>B. ceratocarpa</i> (S; 16.0), <i>B. sp.</i> (L; 24.6), <i>B. succulenta</i> (S; 13.0)
Yanayacu	Napo	00°35' S, 77°53' W	2000–2500	<i>B. borjensis</i> (L; 23.7), <i>B. ceratocarpa</i> (S; 15.2), <i>B. sodiroana</i> (S; 15.8), <i>B. succulenta</i> (S; 13.0)

noseleaf (*i.e.*, the snout), 7–14 mm from the noseleaf (the middle of the head, including the region between the eyes), and 14+ mm from the noseleaf (the forehead). To do this, I created a frame of thin cardboard to place over the slide (outer dimensions 6.5 × 2.5 cm, inner ‘window’ 5.5 × 1.5 cm), which was divided into the previously described regions using hairs that crossed the frame every 7 mm. Two hairs were also affixed parallel to the long axis of the frame to delineate a 1mm strip through the center. Thus, when placed over a slide, this frame marked three rectangles (1 mm wide × 7 mm long), which corresponded to the three regions of the bats’ heads. To facilitate pollen identification, I temporarily lifted the tape and stained the pollen with gelatin cubes containing fuchsin dye (Kearns & Inouye 1993). All pollen grains that occurred in the three regions were counted and classified as being from ‘short’ or ‘long’ species. In two instances, pollen could not be identified to species (*B. succulenta* H. Karst. vs. *B. cylindrocarpa* Zahlbr. in the Bellavista reserve, and *B. succulenta* vs. *B. ceratocarpa* Zahlbr. in the Yanayacu reserve); however, these species are all short-exserted, so this did not affect analyses.

TEST OF HYPOTHESIS 1: SPECIALIZATION ON DIFFERENT-SIZED BATS.—This hypothesis predicts that pollen from long-exserted flowers will be more frequently carried by *A. geoffroyi* (the larger bat), and pollen from short-exserted flowers will be more frequent on *A. caudifer*. To test this, I summed the pollen present in the three regions of the bats’ heads to obtain the total ‘long’ and ‘short’ grains carried by each individual. I then performed a *t*-test to compare the relative proportion of ‘short’ to ‘long’ grains carried by *A. geoffroyi* to that carried by *A. caudifer*. Bats that were not carrying

any *Burmeistera* pollen at the time of capture were not included in this analysis.

TEST OF HYPOTHESIS 2: DIFFERENTIAL POLLEN PLACEMENT.—This hypothesis predicts that pollen from long-exserted and short-exserted flowers will occur on different parts of bats’ bodies. To test this, I conducted a General Linear Model with pollen type (‘short’ or ‘long’) and head region (snout, middle, or forehead) as within-subjects fixed factors and bat type (*A. caudifer* or *A. geoffroyi*) as a between-subjects fixed factor. Individual bats served as the unit of replication, and the dependent variable was the proportion of pollen found in each region (*e.g.*, of all the ‘long’ pollen carried by a bat, the proportion found on the snout vs. middle vs. forehead). Only bats that were carrying both types of pollen were included in this analysis. A significant interaction effect for pollen type by head region would indicate support for the prediction that different exertion lengths deposit on different regions of the head. I included bat type as a factor to determine whether results are different for the different species.

RESULTS

TEST OF HYPOTHESIS 1: SPECIALIZATION ON DIFFERENT-SIZED BATS.—Twenty-six *A. caudifer* and 18 *A. geoffroyi* were captured. Pollen from short- and long- exserted *Burmeistera* was present on the fur of both bat species. On average, *A. caudifer* carried 46.9 ± 13.9 grains of ‘short’ pollen and 485.7 ± 114.9 grains of ‘long’ pollen, while *A. geoffroyi* carried 67.8 ± 31.1 grains of ‘short’ and 750.4 ± 276.3 grains of ‘long.’ The relative proportions of ‘short’ to ‘long’ pollen (Fig. 2) was not significantly different for *A. caudifer* vs. *A. geoffroyi* ($t = -1.26$, $df = 37$, $P = 0.22$). These results do not support the prediction that ‘short’ pollen will be more common on small bats (*A. caudifer*) and ‘long’ pollen on large bats (*A. geoffroyi*).

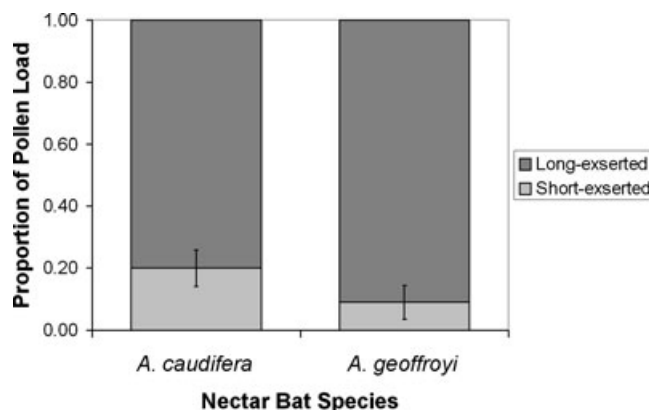


FIGURE 2. Mean proportion of pollen loads on bats’ fur belonging to long-exserted (dark gray) or short-exserted (light gray) species of *Burmeistera* for two bat species: *Anoura caudifer* ($N = 24$) and *A. geoffroyi* ($N = 15$). Error bars indicate one SE.

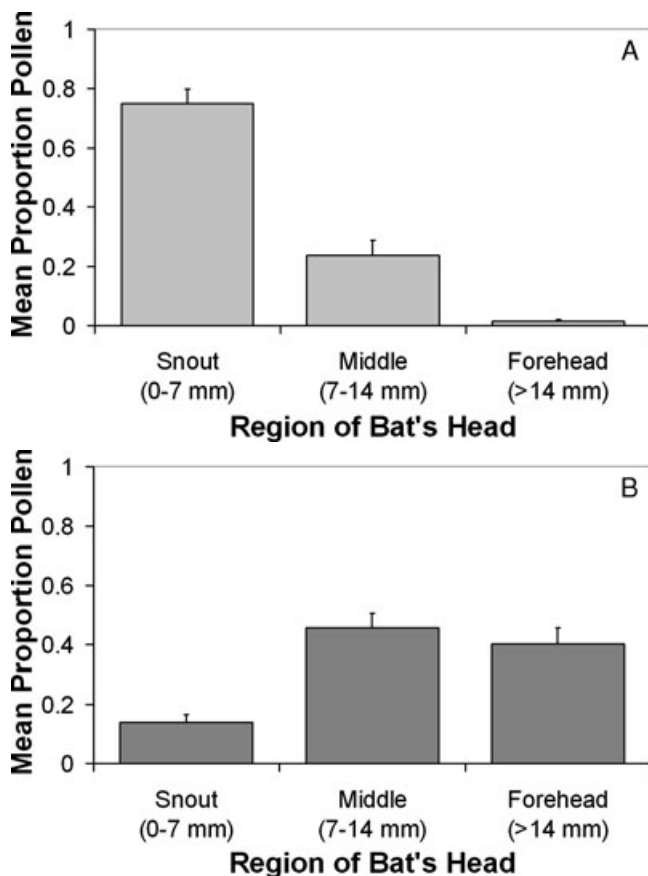


FIGURE 3. The mean proportion of pollen deposited on three regions of the heads of bats (snout, middle, or forehead) for (A) pollen from short-exserted flowers ($N = 28$ bats) and (B) pollen from long-exserted flowers ($N = 37$ bats). Regions were defined by distance from the distal tip of the snout (every 7 mm). Error bars indicate one SE.

TEST OF HYPOTHESIS 2: DIFFERENTIAL POLLEN PLACEMENT.—The General Linear Model found a significant main effect for head region ($F_{2,48} = 7.67$, $P = 0.001$) and a highly significant interaction between pollen type and head region ($F_{2,50} = 29.9$, $P < 0.001$). These results were not different for the two bat species (*A. geoffroyi* or *A. caudifer*), as demonstrated by the lack of a significant interaction between head region and bat type ($F_{2,48} = 0.011$, $P = 0.89$) or a three-way interaction between head region, pollen type, and bat type ($F_{2,48} = 0.06$, $P = 0.94$). Note that because proportions were used, main effects for pollen type or bat type were not analyzed (totals across the three regions always equaled one).

The significant interaction between pollen type and head region demonstrates that the exertion length of a flower (short vs. long) affects where pollen is deposited on bats' heads. 'Short' pollen occurred most frequently on the snout (0–7 mm from noseleaf), less frequently in the middle region (7–14 mm), and only very rarely on the forehead (>14 mm; Fig. 3A). 'Long' pollen occurred most frequently in the middle region and on the forehead, and less frequently on the snout (Fig. 3B). Thus results show that different

degrees of exertion correspond to different sites of pollen transfer on the heads of bats, a key prediction of the hypothesis that the high variation in exertion serves to reduce competition for pollination by spatially partitioning a shared pollinator.

DISCUSSION

Flower morphology varies widely across species of *Burmeistera* in terms of the degree to which the reproductive parts are exerted outside of the corolla (Fig. 1). Results show that this variation does not correspond to specialization on different pollinators. Sympatric species of *Burmeistera* share the locally occurring nectar bats (*A. geoffroyi* and *A. caudifer*) as their primary pollinators. Results instead suggest that variation in exertion length may function to spatially partition bats' heads and thus reduce competition for pollination.

Contrary to the prediction of the first hypothesis, there was no significant difference in the relative proportion of 'short' and 'long' pollen carried by *A. caudifer* versus that carried by *A. geoffroyi* (Fig. 2). Thus the variation in exertion length does not represent specialization on bat species of different sizes. Despite the 20 percent difference in skull length, *A. caudifer* and *A. geoffroyi* can extend their tongues to similar distances (3.7–3.9 cm; Muchhala 2006b). Therefore, even though there might be a selective advantage for sympatric *Burmeistera* to specialize on particular species of *Anoura*, the functional equivalence of these bats (*sensu* Armbruster *et al.* 2000, Gomez & Zamora 2006) probably precludes such specialization. From a bat's perspective, selective pressures should favor being able to feed from all locally available flowers, and it is difficult to imagine an adaptation that might allow a *Burmeistera* flower to exclude the 'unwanted' *Anoura*. The only known instance of floral specialization on one species of bat is in *Centropogon nigricans* Zahlbr. (Campanulaceae); with 8.5-cm corollas, its nectar is only accessible to the extremely long-tongued *A. fistulata* (Muchhala 2006b).

In support of the second hypothesis, exertion length was found to correspond to the placement of pollen on the heads of bats. Pollen from short flowers was found most frequently on the snouts of bats, and pollen from long flowers on the middle or the forehead (Fig. 3). By spatially partitioning pollinator's bodies, variation in exertion length may decrease interspecific pollen transfer and thus reduce competition for pollination among sympatric species of *Burmeistera*. A similar benefit was suggested for bat-pollinated species of *Marcgravia*, which often place pollen in different regions of bats' bodies (Tschapka *et al.* 2006), and for various cooccurring bat-pollinated species in Costa Rica (Howell 1977).

Given the large size of bats relative to other pollinator types, the evolution of differential pollen placement might be expected to be more frequent among flowers pollinated by bats. However, in addition to pollinator size, another factor that will strongly influence whether differential pollen placement evolves is the degree of precision in pollen placement. For *Burmeistera*, the fusion of the anthers into a single anther tube concentrates pollen into a

relatively small spot on the bodies of pollinators, and the fact that the stigma emerges from the center of this tube guarantees that the site of pollen deposition and pick-up are highly correlated. Such a high degree of floral integration, accuracy, and precision (*sensu* Armbruster *et al.* 2004) represents an extreme among plants, comparable with that of the genus *Stylidium* (Stylidiaceae; Armbruster *et al.* 1994, 2004; Armbruster 2006). More generalized, actinomorphic flowers with imprecise pollen transfer would be unable to spatially partition pollinators.

Although further studies would be useful to quantify the competitive pressure, it is a safe assumption that interspecific pollen transfer will have negative impacts on fitness. While traditional mechanisms of competition only operate when the resource in question is limiting, competition for pollination through interspecific pollen transfer operates even when pollinators are abundant. This can be readily seen in terms of male fitness; every grain of pollen that a pollinator loses to heterospecific stigmas or floral parts represents a reduction in potential male fitness (Waser 1983, Campbell & Motten 1985, Armbruster 2006). Female fitness can also be reduced; some studies have found that heterospecific pollen causes the stigma to close prematurely (Waser & Fugate 1986) or clogs the stigmatic surface (Armbruster & Herzig, 1984, Caruso & Alfaro 2000, Brown & Mitchell 2001; but see Kohn & Waser 1985).

Up to four species of *Burmeistera* cooccur in any given cloud forest site, with an average of three species per site (Muchhala 2006a). If bats were randomly distributing pollen among three species, each would be expected to receive on average only 33 percent conspecific pollen (and 66 percent heterospecific); in fact, analysis of pollen deposition on stigmas shows that they receive approximately 80 percent conspecific pollen on average (Muchhala 2006a). I hypothesize that such low levels of interspecific pollen transfer are due in a large part to local divergence in exertion length. Other mechanisms that could decrease interspecific pollen flow include flower constancy of pollinators (Grant 1950, Chittka *et al.* 1999) and clumped distributions of plant individuals (Armbruster *et al.* 1992, Kay 2006); the relative importance of these factors deserves further study.

This study shows that differences in exertion of reproductive parts correspond to differences in pollen placement for *Burmeistera*, which is consistent with the hypothesis that the wide interspecific variation in exertion length represents a response to interspecific competition. However, this hypothesis does not necessarily explain why this variation should be bimodal (Fig. 1). One possibility is that competition may occur most frequently between pairs of species, leading to one increasing and the other decreasing exertion length and an overall bimodal pattern across the genus. Another possibility is that the forehead and snout of a bat (the regions where long and short-exserted flowers place pollen) represent the best locations for pollen placement; perhaps the region between a bat's eyes is less effective for pollen transfer.

Competing species are expected to diverge more in sympatry than allopatry, a process known as character displacement (Dayan & Simberloff 2005). For example, Armbruster *et al.* (1994) found that divergence in pollen placement on shared pollinators by sym-

patric *Stylidium* species in 25 sites was significantly greater than that of randomly generated null models. In my field sites, different populations of *B. sodiroana* diverge in exertion length in a pattern consistent with character displacement. On the western slopes (Bellavista), *B. sodiroana* is abundant and long-exserted (20.1 mm), and cooccurs with three short-exserted species. On the eastern slopes (Yanayacu), *B. sodiroana* is relatively rare and short-exserted (15.8 mm), and cooccurs with *B. borjensis*, which is locally abundant and long-exserted (23.7 mm). While suggestive, data for more species and sites are needed to fully evaluate the extent to which floral character displacement determines assemblage structure of sympatric *Burmeistera*.

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