THE POLLINATION BIOLOGY OF *BURMEISTERA* (CAMPANULACEAE): SPECIALIZATION AND SYNDROMES[1]

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The floral traits of plants with specialized pollination systems both facilitate the primary pollinator and restrict other potential pollinators. To explore interactions between pollinators and floral traits of the genus *Burmeistera*, I filmed floral visitors and measured pollen deposition for 10 species in six cloud forest sites throughout northern Ecuador. Nine species were primarily bat-pollinated (84–100% of pollen transfer); another (*B. rubrosepala*) was exclusively hummingbird-pollinated. According to a principal components analysis of 11 floral measurements, flowers of *B. rubrosepala* were morphologically distinct. Floral traits of all species closely matched traditional ornithophilous and chiropterophilous pollination syndromes; flowers of *B. rubrosepala* were bright red, lacked odor, opened in the afternoon, and had narrow corolla apertures and flexible pedicels, which positioned them below the foliage. Flowers of the bat-pollinated species were dull-colored, emitted odor, opened in the evening, and had wide apertures and rigid pedicels, which positioned them beyond the foliage. Aperture width appeared most critical to restricting pollination; hummingbirds visited wide flowers without contacting the reproductive parts, and bats did not visit the narrow flowers of *B. rubrosepala*. Aperture width may impose an adaptive trade-off that favors the high degree of specialization in the genus. Other floral measurements were highly variable amongst bat-pollinated species, including stigma exsertion, calyx lobe morphology, and pedicel length. Because multiple species of *Burmeistera* often coexist, such morphological diversity may reduce pollen competition by encouraging pollinator fidelity and/or spatially partitioning pollinator's bodies.

Key words: chiropterophily; cloud forests; Ecuador; floral morphology; generalization vs. specialization; Lobelioideae; ornithophily; pollination syndromes.

In tropical rainforests, 98% of angiosperms are estimated to be animal-pollinated (Bawa, 1990). This poses a fundamental problem for tropical plants: How can conspecific pollen transfer be ensured in the midst of the high diversity of heterospecific flowers? The selective pressure to maximize conspecific pollen transfer is thought to have led to the evolution of various mechanisms of partitioning the pollinator resource, including divergence in flowering time (e.g., Stone et al., 1998), differential pollen placement on the bodies of pollinators (e.g., Armbruster et al., 1994), and specialization on different types of pollinators (e.g., Sargent and Otto, 2006).

Since Darwin (1862), biologists have been documenting floral adaptations that facilitate specialization on pollinators. Extensive comparative studies across angiosperm families have revealed suites of floral traits, or pollination syndromes, that correspond to different types of pollinators (Baker, 1961; Pijl, 1961; Stebbins, 1970). However, recent ecological studies suggest that flowers are often visited by diverse assemblages of animals (Herrera, 1996; Ollerton, 1996; Waser et al., 1996). How can ecological generalization be so widespread and yet floral traits suggest extensive evolutionary specialization?

This apparent paradox becomes less surprising when the pool of animals observed to visit a flower is broken down based on the selective pressures they exert on floral phenotype. As a first step, species that are functionally equivalent as pollinators can be grouped together (e.g., bats vs. bees vs. birds; Armbruster et al., 2000). Because of differences in behavior and morphology, often only a subset of the functional groups that visit a flower actually pollinate it. And of this subset, different groups can vary greatly in their effectiveness as pollinators (Schemske and Horvitz, 1984) and in the selective pressures they exert on floral form (Wilson and Thomson, 1996; Aigner, 2001; Thompson, 2001). Some may actually decrease a plant's fitness by "wasting" large amounts of pollen or by decreasing visits of more effective pollinators (Thomson, 2003). Given such variation between pollinators, it is understandable that selective pressures would favor floral specialization on only one functional group out of all of the animals that visit a flower.

Floral traits may function not only to facilitate pollination by the primary pollinator but also to restrict other potential pollinators. Such traits may represent adaptations to prevent ineffective pollinators from "wasting" pollen that would be better transferred by the primary pollinator (Thomson, 2003). For example, red coloration in hummingbird-pollinated flowers may evolve primarily to discourage visitation by bees and thus conserve pollen for hummingbird visits (Raven, 1972). In support of this idea, Schemske and Bradshaw (1999) found that a shift to red coloration in *Mimulus* flowers had no effect on hummingbird visitation but decreased bee visitation by 80%. Traits that restrict pollinators may also represent adaptive trade-offs; that is, in facilitating pollination by one type of pollinator, they sacrifice pollination by another. For example, the narrow tubes of hummingbird-pollinated flowers may be selected for primarily to improve the "fit" between flowers and humming-birds and, in the process, trade off bee pollination by

TABLE 1. List of study sites with locations, elevations, fieldwork dates, and *Burmeistera* species present. All are located in Ecuador; Ecuadorian province is given in parentheses. Pollination studies were carried out on the *Burmeistera* species marked with an asterisk.

Reserve (Province)	Location	Elev. (m a.s.l.)	Fieldwork dates	*Burmeistera* species present
Bellavista (Pichincha)	00°01′S,78°41′W	2000–2400	23 Apr.–2 May 03, 24 Sept.–3 Oct. 03	*B. cylindrocarpa*, B. lutosa*, B. sodiroana*, B. succulenta**
Bilsa (Esmeraldas)	00°21′N,79°43′W	300–700	9–19 Sept. 03	*B. brachyandra, B. crispiloba, B. smaragdi**
Golondrinas (Carchi)	00°50′N,78°07′W	1600–2400	16–27 June 03	*B. cyclostigmata*, B. holm-neilsenii, B. lutosa*, B. multiflora**
Otonga (Cotopaxi)	00°25′S,79°00′W	1300–2300	13–23 Mar. 03	*B. auriculata, B. sodiroana*, B. succulenta*, B. multiflora**
Pahuma (Pichincha)	00°01′N,78°38′W	1700–2600	8–14 July 03, 13–18 Nov. 03	*B. multiflora*, B. resupinata, B. rubrosepala*, B. succulenta**
Yanayacu (Napo)	00°35′S,77°53′W	2000–2500	9–19 May 03, 16–20 Oct. 03	*B. borjensis*, B. ceratocarpa*, B. sodiroana*, B. succulenta**

preventing bees from accessing the nectar (Temeles et al., 2002; Aigner, 2004; Castellanos et al., 2004). Regardless of their evolutionary origins, understanding how such floral traits restrict the potential pollinator pool is critical to understanding specialization in pollination systems.

Here I explore the role of pollinators in the evolution of floral phenotype for the genus *Burmeistera*. While previous research indicates that bats and hummingbirds visit *Burmeistera* flowers, the effectiveness of hummingbirds as pollinators remains unclear (Feinsinger and Colwell, 1978; Stein, 1992; Muchhala and Jarrin-V., 2002; Muchhala, 2003). In this study I filmed flowers to identify all floral visitors and measured pollen deposition on stigmas to quantify the effectiveness of visitors as pollinators. Motivating questions include (1) For each species of *Burmeistera*, percentage of pollen flow is attributable to each functional group of pollinator (bats vs. hummingbirds)? (2) How do floral traits (morphology, exposure, timing of anthesis, color, and odor) relate to these pollination systems? (3) Which of these traits appear to be most important in restricting the potential pollinators?

MATERIALS AND METHODS

Study sites and study organisms—I studied 10 species of *Burmeistera* in six cloud forest reserves throughout the northern Andes of Ecuador. The reserves varied in elevation from 300–2600 m a.s.l., and each contained 3–4 species of *Burmeistera* (Table 1). Fieldwork was carried out from March through November 2003. In total, 15 species were present in the study sites. Voucher collections for each were made and deposited in the herbarium of the Pontificia Universidad Católica del Ecuador. Pollination studies were carried out on those species abundant enough to allow adequate sample sizes, which included: *B. borjensis* Jeppesen, *B. ceratocarpa* Zahlbr., *B. cyclostigmata* Donn. Sm., *B. cylindrocarpa* Zahlbr., *B. lutosa* E. Wimm., *B. multiflora* Zahlbr., *B. rubrosepala* (E. Wimm.) E. Wimm, *B. smaragdi* Lammers, *B. sodiroana* Zahlbr., and *B. succulenta* H. Karst.

Burmeistera belongs to the subfamily Lobelioideae of Campanulaceae (which some authors treat as a separate family, the Lobeliaceae). It contains 105 species distributed from Guatemala to Peru (Lammers, 2006), with a center of diversity in the cloud forests of the Andes of Colombia and Ecuador. In Ecuador alone 35 species occur, of which 22 are endemic (Moreno and Muchhala, 2005). *Burmeistera* are often misclassified as epiphytes, but in fact individuals remain rooted in the ground throughout their lives as either free-standing herbs or hemi-epiphytic herbs or subshrubs that climb nearby vegetation (Jeppesen, 1981). Flowers of *Burmeistera* are zygomorphic; corollas typically have a tubular base that expands distally into a bell shape with the reproductive parts positioned above the opening (Fig. 1). Anthers are fused together to form a tube into which pollen is shed. 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 and Leins, 1995). When fully exserted (normally by the second day), the stigma becomes receptive and the female phase begins. Flowers senesce 6–8 d after anthesis (Stratton, 1989), but stigmas probably lose receptivity earlier; flowers typically angle downwards, and visits stop several days after the female phase begins (N. Muchhala, personal observation). Individual plants remain in flower for

months, with 1–4 flowers open at a time. Full seed set probably requires thousands of pollen grains; hand-pollinated flowers of *B. sodiroana* produced on average 2430 seeds ($\pm$388.9, $N = 8$; N. Muchhala, unpublished data).

Flower visitation—To identify floral visitors, flowers from the 10 species of *Burmeistera* were filmed with Sony (Tokyo, Japan) Nightshot Digital Camcorders. With three cameras, I was able to film three different flowers (from three different plants) at any given time. Each camera was placed on a tripod approximately 2 m away from the focal flower and covered with a modified 2-L plastic bottle to protect it from rain. Flowers were occasionally filmed for more than 1 d, but never past the third day after anthesis. I typically filmed during the day from 1400 to 1800 hours or (less often) from 0700 to 1100 hours and at night from 1830 to 0230 hours (using the Nightshot mode). In total, I filmed 57 different flowers diurnally for 3.6 h on average (range 2–12 h) and 65 nocturnally for 5.7 h on average (range 2–14 h). Visits were defined as an animal entering the corolla of the flower. Segments of film with visits were downloaded to a computer as mpeg files and analyzed for identity of visitors and time and duration of the visit. Duration was recorded as the amount of time the mouthparts of the pollinator remained inserted in the corolla.

Pollen deposition—I measured nocturnal and diurnal pollen deposition on stigmas to quantify effectiveness of visitors in transferring pollen. I located and identified *Burmeistera* plants throughout each reserve and then selected a trail loop with as many individuals as possible. I marked the base of the pedicel of each flower with masking tape and a unique number. I wrapped the flower's reproductive parts (i.e., the stigma and anther tube from which it emerges) with a layer of parafilm, which I left in place throughout the male and female phases of the flower. I then affixed a small rectangle of clear, double-sided plastic tape (10 $\times$ 5 mm) to the parafilm in order to collect pollen brought by floral visitors. I removed and replaced this tape every dawn and dusk to have separate nocturnal and diurnal samples of pollen deposition. These samples were immediately placed on a slide and covered with clear, single-sided plastic tape. In the laboratory, I temporarily lifted the tape and stained the pollen with gelatin cubes containing fuchsin dye (Beattie, 1971). I examined the slides with a light microscope to identify pollen grains present. To quantify pollen deposition, I counted a subset of the pollen grains using the following method. I cut a 5 $\times$ 10 mm hole in the middle of a 15 $\times$ 20 mm square of poster board and affixed hairs in vertical and horizontal transects through the center of the hole. For each slide, I placed this square over the tape sample and counted and identified all pollen grains along the two transects. I was able to identify *Burmeistera* pollen to species, with the exception of two pairs of species with indistinguishable pollen: *B. succulenta* and *B. ceratocarpa* in Yanayacu and *B. succulenta* and *B. cylindrocarpa* in Bellavista. For these species, counts of conspecific pollen deposition may be overestimated. However this does not affect the primary goal of this aspect of the study, which was to compare the relative contributions of nocturnal and diurnal pollinators.

Specialization—I combined the flower visitation and pollen deposition results to estimate the specificity of *Burmeistera* pollination systems. For each flower, I calculated the percentage of total pollen deposition that could be attributed to bats and to hummingbirds. I considered a species of *Burmeistera* that received more than 75% of pollen flow from one type of pollinator to be specialized (sensu Fenster et al., 2004) and in this way categorized each species as (1) specialized to bats, (2) specialized to hummingbirds, or (3) generalized to multiple taxa.

Pollination syndromes—I compared floral traits of species in each of the three categories of specialization to determine whether pollination syndromes
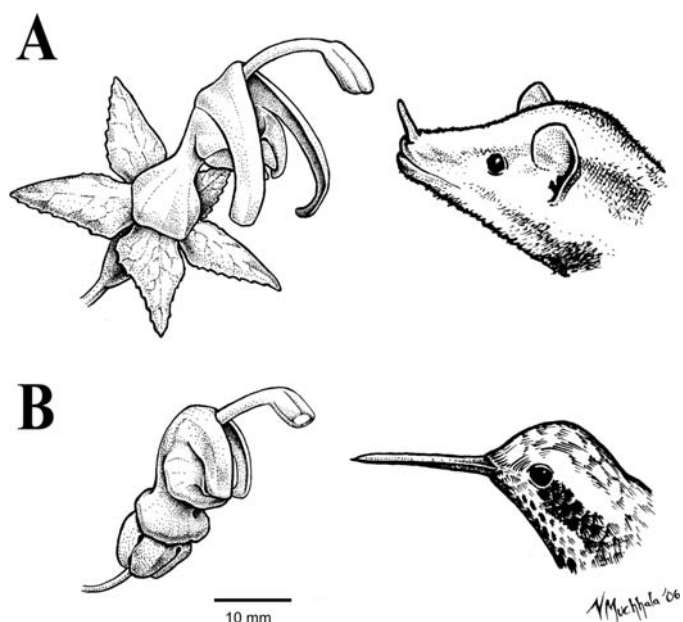
Fig. 1. Illustration of (A) a *Burmeistera borjensis* flower and a bat head (*Anoura geoffroyi*) and (B) a *B. rubrosepala* flower and a hummingbird head (*Adelomyia melanogenys*).

can be identified in the genus. I measured 11 different aspects of floral morphology for each species: greater corolla length (greatest length from corolla base to ends of corolla lobes); lesser corolla length (from base to the split between the two dorsal and three ventral corolla lobes); corolla tube length (from base to corolla flare); corolla tube width (greatest width of corolla tube); outer aperture width (distance between distal ends of dorsal corolla lobes); inner aperture width (width at the split between the two dorsal and three ventral corolla lobes); calyx lobe length (length of the sepal-like calyx lobes), calyx lobe width (greatest width of calyx lobe); pedicel length (from branch to hypanthium), pedicel width (where pedicel attaches to hypanthium), and stigma exsertion (from distal end of corolla tube to center of stigma). I used principal components analysis to explore how the 10 species of *Burmeistera* group in the morphospace defined by these 11 morphological measurements. The analysis was conducted with SPSS for Windows (SPSS Inc., Chicago, Illinois, USA) using standardized data and a matrix of correlations. I also calculated the average flower height for each species (distance from the ground to the flower), and noted flower color, odor, and timing of anthesis. For *B. cyclostigmata*, I was only able to measure the morphology of five flowers and the height of two flowers; for all other species sample sizes ranged from 9 to 41 for morphology and 8 to 38 for height.

RESULTS

Flower visitation—Filming demonstrated that only bats and hummingbirds visit *Burmeistera* flowers regularly. Bat visits occurred only at night (1830–0630 hours), while hummingbird visits occurred only during the day (0630–1830 hours). Several moth visits were recorded at night, but these animals did not contact the reproductive parts of the flowers. I also filmed a rodent that climbed a nearby branch to visit a *B. cylindrocarpa* flower. Such visits are a very rare event, probably because the non-woody branches of *Burmeistera* cannot support the weight of a rodent.

Nine of the 10 species of *Burmeistera* that I filmed received bat visits (Table 2). The majority of these also received hummingbird visits during the day. For these nine species, bats visited somewhat more frequently than hummingbirds on average (0.27 vs. 0.20 visits/h, respectively). The tenth species, *B. rubrosepala,* only received hummingbird visits (0.24 visits/h). These visits were all made by *Adelomyia melanogenys*. Hummingbird visits to the other nine species were mainly made by *A. melanogenys* ($N = 17$) and *Coeligana torquata* ($N = 6$), with occasional visits by *Aglaiocereus coelestis* ($N = 3$), *Haplophaedia lugens* ($N = 1$), and *Phaethornis longirostris* ($N = 1$). Bats could not be reliably identified from videos; however, bat netting demonstrated that *Anoura caudifera* and *A. geoffroyi* (Phyllostomidae: Glossophaginae) visit these flowers (N. Muchhala, unpublished data). Both of these species regularly carry *Burmeistera* pollen and do not discriminate between the various *Burmeistera* species available in a reserve; that is, there is no specialization of *Burmeistera* species to different bat species.

All visits by both bats and hummingbirds were performed while they hovered, with the exception of one visit to *B. multiflora* in which a hummingbird (*A. melanogenys*) landed on the inflorescence and proceeded to probe several flowers. Bat visits were extremely rapid, lasting 0.57 s on average (SD $= 0.31$, $N = 73$), while hummingbird visits averaged 1.22 s (SD $= 1.13$, $N = 45$). Bats and hummingbirds treated flowers differently during visits; hummingbirds typically inserted their bills and accessed the nectar without moving the flowers, while bats always physically displaced them, leaving the flower (and often the whole plant) swinging after a visit. Flowers of *B. rubrosepala* did move slightly during hummingbird visits, angling downwards and causing the reproductive parts to touch the hummingbird's head. During bat visits, the crown of the bat's head always contacted the reproductive parts of the flowers. The crown of *A. melanogenys* individuals always contacted the reproductive parts of *B. rubrosepala* flowers, but only rarely contacted those of other *Burmeistera* species. Because their bills are much longer than *Burmeistera* corollas, *Coeligana torquata* never contacted the reproductive parts of any *Burmeistera* flowers during visits. One of the three recorded visits by *A. coelestis* appeared to be legitimate, while for the other two and the visits by *H. lugens* and *P. longirostris* the hummingbirds failed to contact the reproductive parts.

On several large *B. sodiroana* plants, *C. torquata* were observed to set up territories and visit all flowers in regular cycles. A flower filmed within one of these territories received 7.84 hummingbird visits/h. Because it is an extreme outlier relative to the typical hummingbird visitation rate of 0.20 visits/h, I did not include this flower in the data summarized in Table 2.

Pollen deposition—In Table 3 I report nocturnal and diurnal pollen loads on the stigmas of 10 different species of *Burmeistera* in six different reserves. I summarized the data as mean number of pollen grains per sample (i.e., all pollen, regardless of identity), mean number of conspecific pollen grains per sample, and mean number of heterospecific *Burmeistera* pollen grains per sample. Note that I counted only a portion of total pollen present (along two transects through the center of each sample) to be able to compare relative abundance; total pollen deposition on stigmas was much higher.

Burmeistera rubrosepala was the only species that did not receive pollen nocturnally (Table 3). Diurnally, it received on average 16 conspecific pollen grains per stigma (number of tape samples, $N = 33$). For the other nine species, more pollen was deposited nocturnally than diurnally. Pooling these nine

TABLE 2. Summary of flower filming with mean visitation rates per flower per hour by bats and hummingbirds (HB) to 10 species of *Burmeistera*. Sample size (*N*) is given as the total number of hours filmed (h) and the number of unique flowers filmed (Fls).

	Night				Day			
	N		Bat visits/h		*N*		HB visits/h	
Species	h	Fls	Mean	SD	h	Fls	Mean	SD
B. borjensis	33.6	7	0.13	0.18	21.5	8	0.18	0.35
B. ceratocarpa	28.5	6	0.29	0.29	20.7	7	0.14	0.22
B. cyclostigmata	12.0	1	0.50	—	2.8	1	0.00	—
B. cylindrocarpa	19.2	6	0.04	0.09	11.1	4	0.06	0.19
B. lutosa	48.1	6	0.15	0.18	12.6	4	0.04	0.12
B. multiflora	62.2	7	0.15	0.23	19.4	5	0.07	0.14
B. rubrosepala	31.9	7	0.00	0.00	45.1	6	0.24	0.28
B. smaragdi	40.9	6	0.64	0.76	25.2	5	0.28	0.55
B. sodiroana	30.5	7	0.65	1.08	14.3	7	0.21	0.57
B. succulenta	61.7	12	0.15	0.24	26.5	10	0.42	0.52

species, they received on average 57.4 conspecific pollen grains per night (*N* = 450) and 2.6 conspecific pollen grains per day (*N* = 394).

Although the majority of pollen received by these nine species was conspecific, they also received an average of 13.4 grains of heterospecific *Burmeistera* pollen per night (*N* = 450). This means that approximately four of every five grains of *Burmeistera* pollen deposited were conspecific grains. As might be expected, this ratio was related to the local abundance of each species; when a given species of *Burmeistera* was rare locally, it received less conspecific pollen and more heterospecific pollen. For example, *Burmeistera lutosa* received no conspecific pollen in Bellavista, where it is rare, and an average of 55 grains per sample in Golondrinas, where it is abundant (Table 3). Similarly, *B. multiflora* received only two grains of conspecific pollen per sample in Golondrinas and none in Otonga, while in Pahuma it received 58 conspecific pollen grains per sample (Table 3).

Nocturnal samples also occasionally contained pollen from *Markea*, *Marcgravia*, *Aphelandra*, bromeliads, *Meriania*, and *Passiflora*—all flowers known to be bat-pollinated (Muchhala and Jarrin-V., 2002). Diurnal samples occasionally contained pollen from Ericaceae and Gesneriaceae, as well as several unidentified pollen morphotypes.

Specialization—The results of filming demonstrated that only bats were depositing pollen on *Burmeistera* flowers at night and only hummingbirds during the day. Therefore, the results of nocturnal and diurnal pollen deposition can be used to estimate the relative importance of bats and hummingbirds as pollinators. This demonstrates that none of the species of *Burmeistera* were generalized; all 10 received greater than 75% of pollen flow from one type of pollinator (Table 4). Nine species were primarily bat-pollinated, with bats responsible for 84–100% of observed pollen flow. The remaining species, *B. rubrosepala*, was exclusively pollinated by hummingbirds.

Pollination syndromes—The flowers of the hummingbird-pollinated *B. rubrosepala* differ from those of the nine bat-pollinated *Burmeistera* in a pattern consistent with classic descriptions of ornithophilous and chiropterophilous pollination syndromes (Fig. 1). They are bright, with red corollas and yellow corolla lobes, and lack any odor (as detected by human olfaction). Flowers of the other nine species are dull-colored,

with green corollas shaded by varying amounts of purple or maroon, and emit odors ranging from faint (e.g., *B. succulenta*) to very strong (e.g., *B. borjensis* and *B. multiflora*). For these nine species, flowers opened in the early evening, from 1800 to 2000 hours. I was only able to observe timing of anthesis for two *B. rubrosepala* flowers; both opened in the late afternoon, from 1600 to 1730 hours. All *Burmeistera* flowers remained open for at least 3 d; therefore, timing of anthesis alone did not restrict visitation by bats or hummingbirds.

The flowers of *B. rubrosepala* also differed morphologically from the bat-pollinated species (see Fig. 1). In Table 5, I report means of flower height and the 11 measurements of flower morphology for each species. For the principal components analysis of the 11 measurements of floral morphology, *B. rubrosepala* sits apart in the morphospace defined by the two most important components (Fig. 2). The first component accounted for 37.4% of the variation, the second for 23.7%, and the third for 14.7%. Comparison with a broken-stick null model (Jackson, 1993) demonstrated that only these three components have eigenvalues greater than would be expected by chance, and the third only marginally so. The first component reflects overall flower size, as many variables contributed positively to loading. Those with coefficients whose absolute value is greater than 0.700 included lesser corolla length (0.877), greater corolla length (0.839), tube length (0.823), outer corolla width (0.821), inner corolla width (0.804), and pedicel width (0.785). Because of their small corollas and thin pedicels, this component separates *B. rubrosepala* and the bat-pollinated *B. multiflora* from the other bat-pollinated species. The second component further separates the various bat-pollinated species. Tube width (0.860), sepal width (0.799), and stigma exsertion (0.749) contribute to loading the second component.

To examine flower morphology and flower height in greater detail, I calculated the mean, standard deviation (SD), and coefficient of variation (CV) of each measurement for the nine bat-pollinated species (Table 5). *Burmeistera rubrosepala* is greater than two standard deviations from the mean for five of these 12 measurements: its flowers have narrower apertures (inner and outer aperture width), shorter corolla tubes (tube length), thinner pedicels (pedicel width), and are displayed lower (flower height). Flowers of *B. rubrosepala* also differ in that the outer aperture width is actually smaller than the inner aperture width; rather than flaring outward, the dorsal corolla

TABLE 3.   Analysis of nocturnal and diurnal pollen deposition on stigmas of *Burmeistera* flowers in six reserves in northern Ecuador. Data are given as the mean number of pollen grains present in the tape samples, with standard deviation in parentheses.

| | | | Nocturnal | | | | Diurnal | | |
| | | | | *Burmeistera* pollen | | | | *Burmeistera* pollen | |
Reserve	Species	N	All Pollen	Conspecific	Heterospecific	N	All Pollen	Conspecific	Heterospecific
Bellavista	*B. cylindrocarpa*	48	115 (167.4)	98 (148.8)	13 (35.5)	40	7 (44.7)	5 (33.2)	2 (9.8)
	B. lutosa	4	81 (156.2)	0 (0)	78 (156.5)	2	0 (0)	0 (0)	0 (0)
	B. sodiroana	50	144 (182.1)	100 (152.9)	39 (119)	45	0 (1.2)	0 (1.2)	0 (0)
	B. succulenta	11	9 (30.5)	5 (17.5)	3 (10.3)	8	0 (0)	0 (0)	0 (0)
Bilsa	*B. smaragdi*	59	61 (111.5)	61 (111.2)	0 (0.1)	51	3 (12.6)	2 (12.6)	0 (0)
Golondrinas	*B. cyclostigmata*	8	23 (43.1)	20 (36.5)	0 (0)	5	2 (4.5)	2 (4)	0 (0)
	B. lutosa	35	66 (98.7)	55 (86.2)	2 (9.3)	28	5 (15.2)	5 (15.2)	0 (0)
	B. multiflora	13	19 (37.8)	2 (7.8)	11 (22.4)	10	19 (57.4)	0 (0)	1 (1.3)
Otonga	*B. multiflora*	6	42 (72.7)	0 (0)	42 (72.7)	5	0 (0)	0 (0)	0 (0)
	B. sodiroana	80	62 (117.3)	62 (117.2)	0 (3.4)	71	2 (9.5)	1 (8.3)	0 (0)
	B. succulenta	15	50 (95.4)	29 (77)	18 (48.4)	14	1 (2)	1 (1.5)	0 (0)
Pahuma	*B. multiflora*	30	61 (90.1)	58 (90.6)	1 (3.1)	33	2 (4.2)	0 (0.9)	0 (0)
	B. rubrosepala	39	0 (0)	0 (0)	0 (0)	33	16 (26.5)	16 (26.5)	0 (0)
	B. succulenta	2	107 (151.3)	0 (0)	101 (142.8)	1	0 (−)	0 (−)	0 (−)
Yanayacu	*B. borjensis*	31	62 (90.4)	61 (90.3)	0 (0)	31	6 (21.2)	6 (21.2)	0 (0)
	B. ceratocarpa	32	67 (100.5)	24 (49.4)	43 (75.6)	30	18 (54.3)	5 (14.8)	13 (47.4)
	B. sodiroana	22	59 (93.1)	26 (32)	33 (67)	17	19 (33.3)	9 (20.9)	10 (22.2)
	B. succulenta	4	10 (19.5)	0 (0)	5 (9)	3	3 (4.6)	0 (0)	3 (4.6)

lobes converge to further restrict the corolla opening (Fig. 1). For the nine bat-pollinated species, coefficients of variation differed greatly for the different floral measurements (Table 5). They were smallest for the inner and outer aperture widths (0.09 and 0.14, respectively) and largest for calyx lobe width (0.92), calyx lobe length (0.63), stigma exsertion (0.33), and pedicel length (0.32).

DISCUSSION

The 10 focal species of *Burmeistera* were all highly specialized for pollination by either bats or hummingbirds. For nine species, the nectar bats *Anoura geoffroyi* and *A. caudifera* contributed to greater than 75% of conspecific pollen flow (Table 4). The remaining species, *B. rubrosepala*, was

exclusively pollinated by the hummingbird *Adelomyia mela-nogenys*. These results stress the importance of quantifying the effectiveness of pollinators; although hummingbirds regularly visit the flowers of all 10 species, they only effectively transfer pollen of one. In the following sections, I discuss the close correlation between floral traits and pollinators of *Burmeistera*, the relative importance of these traits in restricting pollinators, and possible implications of the observed variation in floral morphology amongst the bat-pollinated species.

Pollination syndromes—The floral traits of these species appear to have been selected for by the animals that pollinate them and correspond closely to traditional chiropterophilous and ornithophilous pollination syndromes (Baker, 1961; Pijl, 1961; Helversen, 1993). Hummingbirds rely primarily on vision to detect flowers and have no sense of smell;

TABLE 4.   Relative importance of bats and hummingbirds for nocturnal and diurnal conspecific pollen flow to 10 species of *Burmeistera*. Standard deviation is in parentheses. Data is summarized as the percentage contribution by bats and hummingbirds to total pollen transfer.

| | Nocturnal | | Diurnal | | Pollen flow (%) | |
Species	N	Mean pollen transfer	N	Mean pollen transfer	Bats	Hummingbirds
B. borjensis	31	61 (90.3)	31	6 (21.2)	91.1	8.9
B. ceratocarpa	32	24 (49.4)	30	5 (14.8)	84.0	16.0
B. cyclostigmata	8	20 (36.5)	5	2 (4)	94.6	5.4
B. cylindrocarpa	48	98 (148.8)	40	5 (33.2)	95.7	4.3
B. lutosa	39	49 (83.2)	30	4 (14.8)	93.5	6.5
B. multiflora	49	36 (75.9)	48	0 (0.8)	99.6	0.4
B. rubrosepala	39	0 (0)	33	16 (26.5)	0.0	100.0
B. smaragdi	59	61 (111.2)	51	2 (12.6)	96.6	3.4
B. sodiroana	152	69 (124.6)	133	2 (9.9)	97.8	2.2
B. succulenta	32	15 (54.3)	26	0 (1.1)	98.4	1.6

TABLE 5. Mean measurements of flower morphology (in mm) and flower height (in cm) for 10 species of *Burmeistera*. For the nine bat-pollinated species, the overall means (Mean), standard deviations (SD), and coefficients of variation (CV) are also given. See text for explanation of measurements.

| Measurement | Bat-pollinated species | | | | | | | | | HB-poll. | Bat-poll. Summary | | |
	borj	cera	cycl	cyli	luto	mult	smar	sodi	succ	rubr	Mean	SD	CV
Greater corolla length	24.3	26.9	27.4	20.3	22.0	16.5	25.5	24.5	26.6	18.6	23.8	3.6	0.15
Lesser corolla length	16.9	18.4	18.7	16.8	18.5	10.2	17.2	17.0	16.4	11.8	16.7	2.6	0.15
Corolla tube length	14.1	13.2	9.7	12.9	12.8	7.7	14.1	14.0	16.8	7.2	12.8	2.7	0.21
Corolla tube width	10.4	9.8	9.9	6.6	10.3	5.6	6.2	7.6	6.1	10.2	8.0	2.0	0.25
Outer aperture width	17.3	16.3	19.2	14.7	13.0	14.9	18.9	18.9	14.7	1.9	16.4	2.3	0.14
Inner aperture width	7.2	9.2	8.4	7.4	8.3	7.1	7.5	8.3	7.0	3.0	7.8	0.7	0.09
Calyx lobe length	18.2	11.5	6.1	1.9	13.0	4.2	13.7	2.2	12.5	11.8	9.3	5.8	0.63
Calyx lobe width	13.0	2.9	3.6	2.0	3.6	2.2	2.2	3.1	1.7	4.1	3.8	3.5	0.92
Pedicel length	61.5	41.2	74.2	53.9	41.8	40.6	55.3	100.1	64.1	80.5	59.2	19.2	0.32
Pedicel width	2.6	2.0	2.2	3.0	2.1	1.7	2.5	2.6	2.6	1.2	2.3	0.4	0.18
Stigma exsertion	27.3	19.3	29.4	13.9	11.6	17.4	13.7	21.6	14.7	21.1	18.8	6.2	0.33
Flower height	151	99	150	167	87	145	137	153	177	67.3	140.6	29.6	0.21

Note: borj = *B. borjensis*, cera = *B. ceratocarpa*, cycl = *B. cyclostigmata*, cyli = *B. cylindrocarpa*, luto = *B. lutosa*, mult = *B. multiflora*, smar = *B. smaragdi*, sodi = *B. sodiroana*, succ = *B. succulenta*, rubr = *B. rubrosepala*, HB-poll. = hummingbird-pollinated.

correspondingly, flowers of *B. rubrosepala* are brightly colored and lack odor. Bats, which are active nocturnally, rely heavily on olfaction and less on vision to detect flowers; flowers of bat-pollinated *Burmeistera* are dull colored and emit odor nocturnally. Bats treat flowers relatively roughly, as documented by my filming of visits to *Burmeistera*, while hummingbirds typically extract nectar without moving the flowers; correspondingly, bat-pollinated *Burmeistera* have pedicels that are nearly twice as thick as those of *B. rubrosepala*. Only *B. rubrosepala* flowers consistently move during hummingbird visits; they angle slightly down, ensuring that the reproductive parts contact the hummingbird's head. By increasing pedicel flexibility, decreased pedicel width may serve to enhance the effectiveness of hummingbirds as pollinators (sensu Hurlbert et al., 1996). Hovering mechanics also differ between these pollinators: bats flap their wings in an arc that extends well in front of their heads, while hummingbirds keep their wings behind their backs (Helversen, 1993). Therefore, flowers of bat-pollinated *Burmeistera* are well-exposed and high above the ground (mean height = 140.6 ± 29.6 cm), typically projecting vertically or at a 45° angle above the plant's foliage, while flowers of *B. rubrosepala* are oriented horizontally under the leaves and are closer to the ground (67.3 cm). Given that nectar bats echolocate, better exposure may also be important in increasing the acoustic "visibility" of bat-flowers (Helversen and Helversen, 1999). Finally, these pollinator types differ in the morphology of their mouthparts. To ensure proper and consistent placement of pollen, *Burmeistera* flowers must fit their pollinators well. The wide corolla apertures of the bat-pollinated species closely fit bat snouts (Table 5), while the narrow corolla aperture of *B. rubrosepala* matches the relatively thin bills of hummingbirds (Fig. 1). Hummingbirds can access the nectar of wide flowers without touching reproductive parts, as demonstrated by the filming, while narrow flowers may preclude bat visits.

The close match between floral characteristics and pollinators amongst these 10 species of *Burmeistera* suggests pollination syndromes reliably predict pollinators for this genus. During fieldwork in Ecuador, I observed the flowers of an additional 13 species of *Burmeistera*; all correspond closely to the chiropterophilous syndrome. Based on a review of herbarium collections, species descriptions, and keys to *Burmeistera* throughout the neotropics (Wilbur, 1975, 1981; Jeppesen, 1981; Stein, 1987), I conclude that the genus as a whole is primarily bat-adapted, with occasional secondary pollination from hummingbirds as demonstrated for *B. ceratocarpa* (this study) and *B. tenuiflora* (Muchhala, 2003). Apart from *B. rubrosepala*, the Costa Rican *B. parviflora* appears to be the only other nonchiropterophilous species; its small, bright yellow flowers suggest adaption to bee-pollination.

Specialization—Both bats and hummingbirds occur in Ecuadorian cloud forests, and both visit flowers of the bat-pollinated species, yet *Burmeistera* are highly specialized to
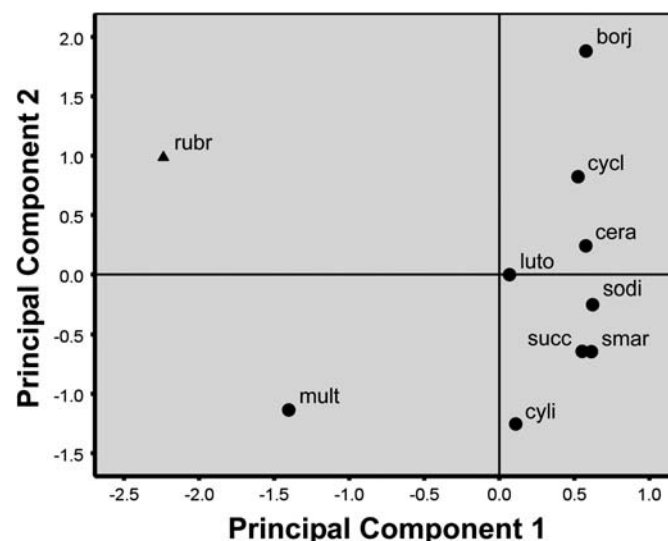

Fig. 2. Floral morphology of 10 species of *Burmeistera* plotted in the two-dimensional morphospace defined by a principal components analysis of 11 floral measurements. The triangle indicates the hummingbird-pollinated *B. rubrosepala* and the circles indicate the nine bat-pollinated species. Species abbreviations are defined in Table 5.

one or the other taxon. Why don't any species of *Burmeistera* generalize to exploit both pollinator types? In considering the evolution of specialized pollination systems, it is useful to decompose the floral phenotype into various floral traits and identify those that serve to restrict the potential pollinator pool (Wilson and Thomson, 1996; Aigner, 2001). For *Burmeistera*, color and odor probably serve primarily to facilitate rather than restrict pollination. That is, bright coloration increases hummingbird pollination without restricting bat pollination, and stronger odor increases bat pollination without restricting hummingbird pollination. Timing of anthesis similarly does not restrict visitation because the flowers remain open for several days and nights. Decreased exposure, in terms of flower accessibility and height, may restrict bat visitation. And pedicel flexibility may restrict both pollinators; bats may be unable to extract nectar from flowers with thin, flexible pedicels while thick, rigid pedicels may decrease hummingbird contact with reproductive parts. However, of all of the floral traits that differ between the ornithophilous and chiropterophilous species of *Burmeistera*, I believe the width of the corolla aperture is the most critical in restricting pollination by bats and hummingbirds and imposes an adaptive trade-off that favors specialization. The ideal width for bat pollination is too wide to ensure that hummingbirds contact the reproductive parts, while the ideal width for hummingbird pollination is too narrow to allow bats access to the nectar. Two lines of evidence support the importance of the inner and outer aperture widths to flower–pollinator fit. First, both measurements are highly constrained amongst bat-pollinated species, with lower coefficients of variation than all other floral measurements (Table 5). Second, they are much smaller for the hummingbird-pollinated species, falling more than six standard deviations outside of the bat-pollinated means (Table 5). I hypothesize that the fit between flower and pollinator is so important for this genus that no intermediate width exists that would adequately exploit both bats' snouts and hummingbirds' bills. Experimental manipulation of width and other floral traits would be useful to verify their influence on bat and hummingbird pollination.

Variation in bat-pollinated flowers—The degree of stigma exsertion has relatively high levels of variation amongst the bat-pollinated species of *Burmeistera* (11.6–29.4 mm, coefficient of variation [CV] = 0.33). This variation may be biologically important if different degrees of exsertion correspond to different sites of pollen transfer on the heads of bat visitors. For sympatric species of plants, sharing a pollinator can reduce fitness due to reproductive interference (i.e., the loss of pollen to foreign stigmas and stigma clogging by foreign pollen; Rathcke, 1983). Variation in the site of pollen placement is one way to alleviate this cost (Nilsson et al., 1987; Armbruster et al., 1994). In each of the study sites, three species of *Burmeistera* coexist on average (range 1–4 species; Table 3). If bats were randomly distributing pollen between three co-occuring species, each would be expected to receive 33% conspecific and 66% heterospecific pollen. Results show that they actually receive approximately 80% conspecific and only 20% heterospecific pollen on average. Local divergence in the degree of stigma exsertion may contribute to such low levels of heterospecific pollen transfer.

The morphology of the calyx lobes also varies greatly between bat-pollinated species, in terms of width (1.7–13.0 mm, CV = 0.92) and length (1.9–18.2 mm, CV = 0.63) as well as the margin (entire, sinuate, or dentate) and the angle relative to the corolla (erect, patent, or reflexed). A somewhat speculative hypothesis for this remarkable diversity is that it also serves to alleviate reproductive interference, in this case by encouraging pollinator fidelity. Calyx lobes likely function as a visual or acoustic signal for bats, facilitating detection of flowers of *Burmeistera* amidst background foliage. For many animals, it has been demonstrated that the experience gained in detecting a cryptic food item leads to formation of a "search image" to better detect these same items later (Langley, 1996; Zentall, 2005). If flowers of all local species of *Burmeistera* appeared identical, after visiting the flower of one species and learning that it contains nectar, a bat would be just as likely to visit a heterospecific *Burmeistera* next. If flowers appeared different for each species, a bat would be more likely to develop a distinct search image and follow with a visit to another individual of the same species. In this way, divergence in calyx lobe morphology may serve to encourage fidelity of individual bats despite infidelity of the species as a whole. Divergence in morphology of corolla lobes would likely achieve a similar effect, but these structures are less evolutionarily labile because of their functional role in protecting the reproductive parts of developing flowers prior to anthesis and in regulating the "fit" between bat and flower after anthesis.

Finally, the relatively high variation in pedicel length (40.6–100.1 mm, CV = 0.32) reflects different methods of spatially separating flowers and foliage to increase flower accessibility. The two free-standing herbaceous species (*B. multiflora* and *B. lutosa*) have some of the shortest pedicels (40.6 and 41.8 mm, respectively); because flowers only occur on the tops of vertical stems, these lengths are adequate to position them beyond the plant's foliage. The climbing hemi-epiphytic species (*B. cyclostigmata*, *B. cylindrocarpa*, *B. borjensis*, *B. succulenta*, and *B. smaragdi*) have flowers that intersperse with leaves along horizontal branches; for these species, longer pedicels (53.9–74.2 mm) serve to raise flowers above the leaves at 45° angles. *Burmeistera sodiroana* is also hemi-epiphytic, but its flowers hang below the branches on extremely long pedicels (100.1 mm), which position them horizontally beyond the leaves (see cover photo). Flowers of the hummingbird-pollinated *B. rubrosepala* hang below the branches in a similar fashion, but shorter pedicels (80.5 mm) place the flowers under rather than beyond the leaves. *Burmeistera ceratocarpa* is sometimes herbaceous and sometimes hemi-epiphytic and has evolved a unique solution to increase accessibility for bats. Wherever flowers occur, leaves are much smaller than elsewhere on the plant; herb-like pedicel lengths (41.2 mm) suffice to position the flowers beyond these leaves.

Conclusions—This study demonstrates high specificity in the pollination systems of *Burmeistera* and provides another example of the varied and often highly specialized pollination modes of tropical plants (e.g., Nilsson et al., 1987; Armbruster, 1993; Johnson and Steiner, 1997; Kay and Schemske, 2003). The close match between floral traits and pollinators in this genus supports the predictive power of the traditional chiropterophilous and ornithophilous pollination syndromes. Of the traits that differ between these syndromes, the width of the corolla aperture appears most important for restricting the potential pollinator pool and may impose a trade-off that favors specialization. While floral width varies little amongst the bat-pollinated species of *Burmeistera*, the degree of stigma

exsertion and the morphology of calyx lobes are highly variable. Divergence in these traits may reduce heterospecific pollen transfer and thus facilitate the coexistence of multiple species. This study highlights various aspects of the floral phenotype that may have been shaped by pollinator-mediated selective pressures; experimental manipulations of floral traits would be useful to verify these proposed selective pressures.

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