Letter

Making yourself heard: why well-exposed flowers are an adaptation for bat pollination

Introduction

Botanists have long recognized that the traits of a flower can often be used to predict its primary pollinator and began formalizing descriptions in the middle of the 20th century of suites of traits, or pollination syndromes, associated with each pollinator type (Vogel, 1954; van der Pijl, 1961). These traits tend to evolve together during evolutionary shifts to different pollinators, and similar suites of traits will convergently evolve in distantly related taxa (Fenster *et al.*, 2004; Dellinger, 2020). For instance, the syndrome of chiropterophily, or adaptation to pollination by bats, includes flowers with wide, bell-shaped corollas, dull coloration, musty odors, and copious pollen, which are well-exposed relative to the rest of the plant's foliage (Vogel, 1958; von Helversen, 1993; Fleming *et al.*, 2009). The consistent appearance of many of these traits in association with bat pollination strongly suggests an adaptive significance, and in some cases, experimental work confirms this assumption. For instance, wide flowers help to guide bats during visits to ensure consistent pollen placement on specific regions of their heads (Muchhala, 2007), and strong sulfuric scents help to attract bats (von Helversen *et al.*, 2000). Additionally, experiments suggest that copious pollen production is selected for due to the fact that bat fur can carry more pollen than feathers or insect bodies, leading to male–male competition, which favors increased pollen production per flower (Muchhala & Thomson, 2010). However, the adaptive significance of well-exposed flowers remains obscure.

Chiropterophilous plants achieve this increased exposure through various methods. Some woody plants position their flowers on the main trunk or branches (termed 'cauliflory'), as seen in *Crescentia cujete* (Diniz *et al.*, 2019). Many epiphytes and lianas hang their flowers below the foliage on long rope-like stems ('flagelliflory'), such as *Mucuna holtonii* (von Helversen & von Helversen, 1999) and *Weberocereus tunilla* (Tschapka *et al.*, 1999). And bat-pollinated herbs and shrubs frequently position their flowers above their foliage ('styliflory') via a tall central flowering stalk, such as *Aphelandra acanthus* (Muchhala *et al.*, 2009) and *Werauhia gladioliflora* (Tschapka & von Helversen, 2007), or via long floral stems (pedicels), such as *Adenocalymma dichilum* (Domingos-Melo *et al.*, 2023) and *Burmeistera borjensis* (Muchhala, 2006). A phylogenetic comparative analysis across *c.* 24 shifts between bat and hummingbird pollination in the centropogonid clade (*Burmeistera*, *Sipho-campylus*, and *Centropogon*) of Campanulaceae demonstrates how

consistent this difference in floral exposure is; stem length predicts pollination syndrome closely, with stems of bat-adapted flowers averaging 70% longer than those of hummingbird-adapted ones (Lagomarsino *et al.*, 2017).

What might select for increased exposure in bat-adapted flowers? One possibility involves flight kinematics, in that bats move their wings forward in wide arcs around and in front of their bodies during hovering flight, while hummingbirds keep their wings to the sides and behind the body (Baker, 1961; von Helversen, 1993). A second possibility is that this represents selection to reduce predation risk for the bats, as snakes or predatory mammals (see Hopkins & Hopkins, 1982) would not be able to hide close to the flowers. A final possibility is that the increased exposure serves to increase detection by foraging bats. While these three hypotheses are not mutually exclusive, only the third makes the testable prediction that bats will take longer to find flowers that are not as well exposed.

The hypothesis that increased floral exposure evolves to maximize detection becomes even more plausible considering that New World nectar-feeding bats rely heavily on echolocation to find their flowers (Gonzalez-Terrazas *et al.*, 2016a,b). For an echolocating animal, background clutter echoes can readily mask echoes of target objects (Schnitzler *et al.*, 2003). While insectivorous bats that forage in narrow spaces can overcome this problem by relying on cues from the movement of their prey items or sounds they produce (Arlettaz *et al.*, 2001; Denzinger *et al.*, 2018), nectar-feeding bats need to be able to locate an immobile target. Thus, we would predict that the more plants can separate flowers from clutter echoes, the greater the chance of bats finding these flowers. In support of this idea, it was found that greater amounts of obstruction around *Burmeistera* flowers significantly decreased bat pollination but had no effect on hummingbird pollination of the same flowers (Muchhala, 2003).

In the present study, we experimentally test the hypothesis that increased exposure will decrease foraging times. We present wild-caught nectar bats with short or long-stemmed flowers in flight cages and time how long it takes them to find the flower. To overcome their well-developed spatial memory (Thiele & Winter, 2005; Carter *et al.*, 2010), we constantly rotate flower position randomly between trials, ensuring each involves a new search. We repeat experiments in simple backgrounds, lacking clutter echoes from foliage, and complex backgrounds, where flowers are presented surrounded by branches and leaves, to determine whether stem length itself influences search time or whether it interacts with background clutter.

Materials and Methods

This study was conducted from 8 to 24 June 2019, in the private reserve Zingara (3.540°N, 76.605°W), in the Valle de Cauca

Department of Colombia. Zingara forms part of the Key Biodiversity Area (KBA) Bosque de San Antonio, and consists of 3.15 ha of cloud forest at 1800–2000 m elevation. To capture nectar-feeding bats, each night we placed four to eight mist nets (of varying lengths, from 2 to 12 m) along potential bat flyways and in front of *Burmeistera* flowers, which are known to be pollinated by bats (Muchhala & Potts, 2007). All bats were identified, weighed, and immediately released except for individuals of *Anoura caudifer* (Geoffroy Saint-Hilaire 1818). We also captured several *Glossophaga soricina* (Pallas, 1766), another nectar-feeding bat, but opted to focus our experiments on the *A. caudifer* because of its abundance. These were then placed individually in one of three screen tents (3 m² × 2 m high) set up in a field next to the research station, and for the first night, were allowed to habituate to the cages and feed *ad libitum* from 20% sugar water solutions. Sugar water was placed in 50 ml polypropylene centrifuge tubes, which were affixed to poles in the cage using plastic-covered wire. Bats that did not learn to hover-feed from these tubes within 3 h after capture were released to minimize the risk of starvation (nectar bats have high nightly energy requirements, and need to visit an estimated 100 flowers per night to meet them; Voigt *et al.*, 2006); those that did feed were held for another 2 d for experimental trials.

For the foraging experiments, a single flower was presented to the bat per trial in order to record the time until feeding. We used freshly collected flowers of *Burmeistera succulenta* H. Karst & Triana (Supporting Information Fig. S1), surrounding the stem (trimmed to *c.* 2 cm length) in cotton and placing it in a 1.5 ml microcentrifuge tube. Caps were removed from the tubes, and they were filled with water and then covered with a piece of duct tape to hold the flower in place. Plastic-covered wire was then used to fashion new 'stems' of two different sizes: 10 or 20 cm. The stem length of *Burmeistera* flowers can vary from 2.2 to 14.5 cm (N. Muchhala, unpublished); we chose these lengths to maximize differences in our experiment. One end of the wire was spiraled around the base of the centrifuge tube, but not affixed with tape, allowing the same flower to be easily switched between long and short 'stems'. The other end was spiraled around one of four wood poles set up in the screen tent, such that the flower was positioned either 10 or 20 cm away from the pole. The four 1.5-m-tall poles were arranged in a square pattern, 1 m away from each other. Background clutter was manipulated to present the flowers in two treatments: simple, with no vegetation added to the poles, and complex, with leaves arranged around the tops of the poles (Fig. S2). Specifically, for complex, we placed two fern leaves along the middle of each pole and three Melastomataceae branches (*Pleroma heteromallum*) at the top (two pointed outwards in a V shape and one pointed upwards; see Fig. 1).

For each of 10 *A. caudifer* individuals, experimental trials were run in simple backgrounds for the first day and complex backgrounds on the second day. We randomly selected long or short stems for the first trial, and then alternated between these for a total of 20 trials. We noticed that variation in visit time was very large for the initial trials, likely as bats were getting accustomed to the flight cage and the experimental array; thus, we opted to treat the first 10 trials of each day as habituation time and only use the last 10 trials for experimental analyses. For each trial, we refilled the

Fig. 1 Nectar bat (*Anoura caudifer*) visiting a flower (*Burmeistera succulenta*) in an experimental trial with a complex background. Photograph by Andrea Bernal.

flower with 20% sugar water using a syringe and then randomly selected one of the poles (using a die) to place it on. After the initial trial, we selected one of the three poles that had not been used in the previous trial to avoid repeating the position. We then rolled the die again to randomly select horizontal orientation angle (where 1 = 30°, 2 = 60°, ... 6 = 360°) and affixed the wire 'stem' to the pole. We positioned the stem roughly parallel to the ground (at the predetermined horizontal angle relative to the screen tent's door), with the tube and flower held upwards at a roughly 75° angle relative to the horizon (mimicking the natural positioning of *Burmeistera* stems and flowers). Once the flower was set up, we began recording the timing of events, noting the beginning of the trial and each time the bat started or stopped flying (i.e. by perching on the sides or top of the tent). One experimenter tracked bat activity with a headlamp, while the second experimenter recorded events, using a stopwatch cellphone app to take times. We ended the trial when the bat visited the flower (Video S1). At any point in the experiment if the bat remained perched for > 5 min, we gently tapped the screen next to the bat to encourage further flight. Trials in simple and complex backgrounds followed the same procedure, except that in complex backgrounds we also rotated all four poles clockwise by 30° between trials to further reduce bats' reliance on spatial memory while foraging.

For our statistical analyses, we used the duration of the last flight in each trial (from perching until visiting the flower) as the response variable. We used a generalized linear mixed model (GLMM; Bolker *et al.*, 2009) to test the influence of stem length, background type, and their interaction on time until visitation in this last flight. We used the LME4 (Bates *et al.*, 2015) and GLMMTMB (Brooks *et al.*, 2017) packages to compare the fit of negative binomial and Poisson error distributions; both AIC and likelihood-ratio tests found the former a better fit. We checked model diagnostics using the packages DHARMA (Hartig, 2022) and PERFORMANCE (Lüdecke *et al.*, 2021); both found no deviation from the expected distribution of residuals, overdispersion, or significant outlier effects. Thus, for our final analysis,

Table 1 Results of the generalized linear mixed model (GLMMs) for bat foraging experiments testing effects of stem length (short or long) and background (simple or complex) on time to locate flowers, including an additive model with both factors and an interactive model with both factors and their interaction, with significant *P*-values indicated in bold.

Model type	Model term	Estimate	SE	Z value	P-value	Lower 95% CI	Upper 95% CI
Additive	Intercept	3.300	0.126	26.20	< **0.001**	3.050	3.550
	Stem length	−0.291	0.128	−2.28	**0.023**	−0.543	−0.040
	Background	0.045	0.128	0.35	0.724	−0.205	0.295
Interactive	Intercept	3.130	0.133	23.50	< **0.001**	2.870	3.400
	Stem length : Long	0.028	0.177	0.16	0.876	−0.321	0.376
	Background : Complex	0.360	0.176	2.05	**0.041**	0.014	0.705
	Interaction	−0.637	0.251	−2.54	**0.011**	−1.130	−0.144

we specified a negative binomial error distribution and a log link function for the model, with stem length (long vs short), background type (simple vs complex), and their interaction as fixed effects, and individual bat identity as a random factor. The trial sequence number was also used as a random factor to control for the fact that bats may improve at the task of finding flowers as the experiment progresses. We calculated 95% confidence intervals around the model estimates using the *tidy* function from the BROOM.MIXED package (Bolker & Robinson, 2022). As the interaction between background type and stem length was significant, we also performed *post hoc* contrasts to assess differences between the four combinations of stem length and background type using the Bonferroni *P*-value correction for multiple comparisons in the package EMMEANS (Lenth, 2024). We performed analyses using the R statistical software v.4.2.2 (R Development Core Team, 2022) and provided the raw data (Dataset S1) and an annotated R script used for these analyses (Notes S1).

Results

Our initial GLMM analysis showed that stem length had a small but significant effect on the response, in that long stems led to decreased foraging times, while background type showed no effect (see Additive Model, Table 1). A follow-up GLMM that included both factors and an interaction effect (see Interactive Model, Table 1) detected a significant effect of the interaction between stem length and background type. Specifically, there was no clear difference in foraging time for short vs long stems in simple backgrounds (23.1 ± 23.3 SD vs 24.1 ± 22.1 SD; Fig. 2), but nearly double foraging time for short vs long stems in complex backgrounds (33.4 ± 29.8 SD vs 18.1 ± 18.17 SD). *Post hoc* contrasts are concordant with these results, showing that foraging time in simple vs complex backgrounds are not significantly different for short stems ($Z = −2.10$, $P = 0.14$) or for long stems ($Z = 1.61$, $P = 0.42$), and that foraging time for short vs long stems is not significantly different in simple backgrounds ($Z = −0.28$, $P = 1.00$), but it is significantly different in complex backgrounds ($Z = 3.44$, $P = 0.0024$).

Discussion

The nectar-feeding bats in our flight cage experiments took more time to locate flowers with short floral stems (pedicels) than those
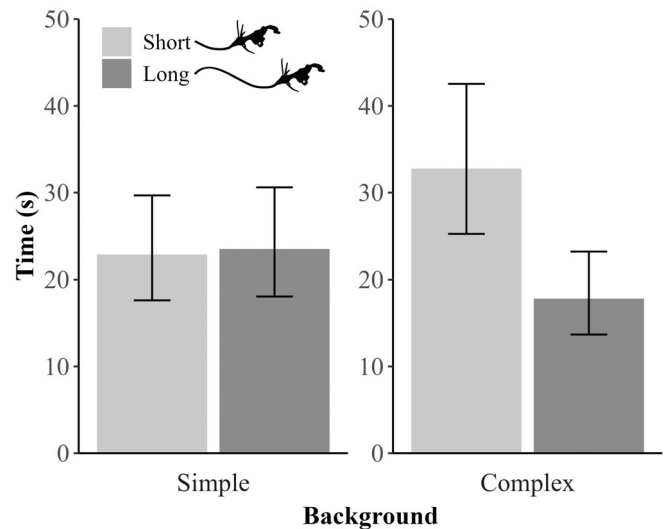

Fig. 2 Time, in seconds, until nectar bats (*Anoura caudifer*) find and visit the experimental flower (*Burmeistera succulenta*) in their last foraging flight. Trials were repeated in simple (no foliage) and complex (with foliage) backgrounds, for flowers presented on short or long floral stems (pedicels). Bars show the least square means from the best-fitted generalized linear mixed model (e.g. with both main effects and their interaction), and error bars represent 95% confidence intervals. *Post hoc* tests show that foraging time for short vs long stems is not significantly different in simple backgrounds ($Z = −0.28$, $P = 1.00$; left panel), but it is significantly different in complex backgrounds ($Z = 3.44$, $P = 0.0024$; right panel). Additionally, foraging time in simple vs complex backgrounds are not significantly different for either short stems ($Z = −2.10$, $P = 0.14$; light gray bars) or for long stems ($Z = 1.61$, $P = 0.42$; dark gray bars).

with long stems. This demonstrates the importance of well-exposed flowers in decreasing bat foraging times. The fact that short stems led to nearly double the foraging time in complex backgrounds cluttered with vegetation, but have no detectable effect in simple backgrounds without vegetation, demonstrates that it is not stem length *per se* that is driving this pattern. Rather, long stems only reduce foraging time in cluttered backgrounds, supporting the idea that stem length aids detection because it separates flowers from background foliage.

Our experimental results support an adaptive hypothesis for why bat-pollinated flowers tend to be so well-exposed beyond the rest of the foliage. By reducing bat foraging times, increased exposure directly benefits these flower's mutualists. In turn,

better-exposed flowers will be located more quickly and thus likely receive more visits through anthesis, leading to increased pollen export and receipt. And perhaps most importantly, the better exposed that a flower is, the greater the chance it is found at all by pollinators; flowers that remain undetected will, of course, fail to reproduce. The importance of effective cues to maximize detection can also be seen in experiments by von Helversen & von Helversen (1999), which showed that the curved upper petal of *M. holtonii* flowers serves as an acoustic guide for nectar bats and that removal of this petal decreases visitation from 88% to only 21%.

We suggest that the main reason long stems aid bats in finding flowers, while they do not seem to be as important for hummingbird or insect pollination, has to do with bat reliance on echolocation while foraging. Ears cannot localize the source of sound waves as precisely as eyes can localize the source of light waves, as each ear has a single eardrum, while each eye has multiple photoreceptors, which together provide a two-dimensional image. Thus, any other sources of echoes close to a focal object will obscure it, creating unwanted 'clutter echoes' (*sensu* Schnitzler *et al.*, 2003), which overlap with target echoes. When foraging in clutter, insectivorous bats have been found to shift to increased reliance on vision (Eklöf *et al.*, 2002), and nectar bats will shift to greater reliance on scent (Muchhala & Serrano, 2015), in line with the idea that echolocation becomes a less reliable sensory modality in such situations. Interestingly, rather than moving the flower away from its vegetative parts, another evolutionary approach to reduce clutter echoes found in bat-pollinated cacti is the evolution of wooly hairs around the flowers that absorb ultrasound, thus making the floral echoes more apparent (Simon *et al.*, 2023).

It is possible that other sensory modalities, such as olfaction or vision, may contribute to the observed decrease in foraging time for long stems. For instance, flowers of *B. succulenta* emit a musty odor; it is possible that greater flower exposure enhances odor plumes (*sensu* Vickers *et al.*, 2001), via interactions with air movement through foliage, such that long stems aid in emitting odor cues. Additionally, we note that our experiments were conducted in relatively well-lit conditions, due to our headlamps, moonlight, and light pollution from streetlamps; thus, the bats may also have been relying on vision while foraging. It would be illuminating to repeat the experiments in different light levels, from the equivalent light of a full moon to zero light (using infrared cameras to document bat behavior). We predict that the patterns we documented would be even more exaggerated in low-light conditions, such as during a new moon and/or deep in the forest understory, where bats would need to rely solely on echolocation rather than vision. Thus, the benefit of long stems may be due to some combination of enhanced visual, olfactory, or echo cues, which further experiments could help to tease apart.

One potential confounding variable in our experimental design was that we always ran simple-background trials on the first day and complex–background trials on the second day of our experiments. In fact, previous work does suggest that nectar bats are able to learn and improve performance in tasks through time (Muchhala & Serrano, 2015). However, any such learning would be expected to lead to bats finding flowers more quickly; the fact that they took longer to find the flowers in complex backgrounds on the second day suggests that the increased difficulty of the task outweighed any learning effects (and perhaps that the effect size would have been even more pronounced if the order were reversed).

In conclusion, among the three hypotheses outlined in the introduction for the evolution of well-exposed flowers, our results support the idea that exposure increases apparency, making the flowers easier to detect via echolocation. Results do not support the hypothesis that long stems evolved to accommodate bat wing kinematics; bats in our experiments were able to hover effectively in front of the flower for both our long and short-stemmed treatments. Results similarly fail to support the idea that long stems evolve to minimize predation risk, as this does not seem likely to explain why there is a difference in locating the flowers in complex backgrounds and not in simple backgrounds. While it might be argued that the longer time before visits to long-stemmed flowers was due to bats investigating and hovering in front of flowers longer due to perceiving a greater predation risk, anecdotally we did not notice such an effect. The time difference between long and short-stemmed flowers was due to time spent searching among the four poles, not to exploratory flights around the pole with the flower after it was located. Instead, our results suggest that by increasing flower exposure through long stems or other means, plants separate their flowers from background clutter echoes from their own foliage and surrounding foliage that could otherwise obscure the flowers for echolocating animals. We expect strong selection on this trait, as it reduces the amount of time bats need to find these flowers, and perhaps more importantly, increases the chances that a given flower will be found at all. Overall, this provides an adaptive explanation for the well-documented pattern of highly exposed flowers among bat-pollinated plants, as noted in classic descriptions of the chiropterophilous pollination syndrome.

Competing interests

None declared.

Author contributions

NM conceptualized the project, designed the experiments, and wrote the manuscript, JM-H aided in data analysis and interpretation. AZ aided in logistics and acquisition of data. All three coauthors contributed to experimental design and manuscript revisions.

ORCID

Juan Moreira-Hernández (iD) https://orcid.org/0000-0003-4328-8094
Nathan Muchhala (iD) https://orcid.org/0000-0002-4423-5130
Alejandro Zuluaga (iD) https://orcid.org/0000-0002-5874-6353

Data availability

Raw data are available in Dataset S1.

Nathan Muchhala[1]* (iD) , **Juan Moreira-Hernández**[1] (iD)
and Alejandro Zuluaga[2] (iD)

[1]Department of Biology, University of Missouri – St Louis, St Louis, MO 63121, USA;
[2]Departamento de Biología, Universidad del Valle, Cali, 760042, Colombia
(*Author for correspondence: email muchhalan@umsl.edu)

References

Arlettaz R, Jones G, Racey PA. 2001. Effect of acoustic clutter on prey detection by bats. *Nature* 414: 742–745.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using LME4. *Journal of Statistical Software* 67: 1–48.

Bolker B, Robinson D. 2022. BROOM.MIXED: tidying methods for mixed models. [WWW document] URL https://github.com/bbolker/broom.mixed [accessed 4 July 2024].

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24: 127–135.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM. 2017. GLMMTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9: 378–400.

Carter GG, Ratcliffe JM, Galef BG. 2010. Flower bats (*Glossophaga soricina*) and fruit bats (*Carollia perspicillata*) rely on spatial cues over shapes and scents when relocating food. *PLoS ONE* 5: e10808.

Dellinger AS. 2020. Pollination syndromes in the 21st century: where do we stand and where may we go? *New Phytologist* 228: 1193–1213.

Denzinger A, Tschapka M, Schnitzler HU. 2018. The role of echolocation strategies for niche differentiation in bats. *Canadian Journal of Zoology* 96: 171–181.

Diniz UM, Domingos-Melo A, Machado IC. 2019. Flowers up! The effect of floral height along the shoot axis on the fitness of bat-pollinated species. *Annals of Botany* 20: 1–10.

Domingos-Melo A, Albuquerque-Lima S, Diniz UM, Lopes AV, Machado IC. 2023. Bat pollination in the Caatinga: a review of studies and peculiarities of the system in the new world's largest and most diverse seasonally dry tropical forest. *Flora* 305: 152332.

Eklöf J, Svensson AM, Rydell J. 2002. Northern bats, *Eptesicus nilssonii*, use vision but not flutter-detection when searching for prey in clutter. *Oikos* 99: 347–351.

Fenster CB, Armbruster WS, Wilson P, Dudash MR, Thomson JD. 2004. Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution, and Systematics* 35: 375–403.

Fleming TH, Geiselman C, Kress WJ. 2009. The evolution of bat pollination: a phylogenetic perspective. *Annals of Botany* 104: 1017–1043.

Gonzalez-Terrazas TP, Koblitz JC, Fleming TH, Medellín RA, Kalko EK, Schnitzler HU, Tschapka M. 2016a. How nectar-feeding bats localize their food: echolocation behavior of *Leptonycteris yerbabuenae* approaching cactus flowers. *PLoS ONE* 11: e0163492.

Gonzalez-Terrazas TP, Martel C, Milet-Pinheiro P, Ayasse M, Kalko EK, Tschapka M. 2016b. Finding flowers in the dark: nectar-feeding bats integrate olfaction and echolocation while foraging for nectar. *Royal Society Open Science* 3: 160199.

Hartig F. 2022. DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package v.0.4.6. [WWW document] URL http://florianhartig.github.io/DHARMa/.

von Helversen D, von Helversen O. 1999. Acoustic guide in bat-pollinated flower. *Nature* 398: 759–760.

von Helversen O. 1993. Adaptations of flowers to the pollination by glossophagine bats. In: Barthlott W, Naumann CM, Schmidt-Loske K, Schuchmann KL, eds. *Animal–plant interaction in tropical environments*. Bonn, Germany: Museum Koenig, 41–59.

von Helversen O, Winkler L, Bestmann HG. 2000. Sulphur containing "perfumes" attract flower-visiting bats. *Journal of Comparative Physiology A* 186: 143–153.

Hopkins HC, Hopkins MJ. 1982. Predation by a snake of a flower-visiting bat at *Parkia nitida* (Leguminosae: Mimosoideae). *Brittonia* 34: 225–227.

Lagomarsino LP, Forrestel EJ, Muchhala N, Davis CC. 2017. Repeated evolution of vertebrate pollination syndromes in a recently diverged Andean plant clade. *Evolution* 71: 1970–1985.

Lenth R. 2024. EMMEANS: estimated marginal means, aka least-squares means. R package v.1.10.3. [WWW document] URL https://rvlenth.github.io/emmeans/.

Lüdecke D, Ben-Shachar MS, Patil I, Waggoner P, Makowski D. 2021. PERFORMANCE: an R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software* 6: 3139.

Muchhala N. 2003. Exploring the boundary between pollination syndromes: bats and hummingbirds as pollinators of *Burmeistera cyclostigmata* and *B. tenuiflora*. *Oecologia* 134: 373–380.

Muchhala N. 2006. The pollination biology of *Burmeistera* (Campanulaceae): specialization and syndromes. *American Journal of Botany* 93: 1081–1089.

Muchhala N. 2007. Adaptive trade-off in floral morphology mediates specialization for flowers pollinated by bats and hummingbirds. *The American Naturalist* 169: 494–504.

Muchhala N, Potts MD. 2007. Character displacement among bat-pollinated flowers of the genus *Burmeistera*: analysis of mechanism, process, and pattern. *Proceedings of the Royal Society B* 274: 2731–2737.

Muchhala N, Caiza A, Vizuete JC, Thomson JD. 2009. A generalized pollination system in the tropics: bats, birds, and *Aphelandra acanthus*. *Annals of Botany* 103: 1481–1487.

Muchhala N, Serrano D. 2015. The complexity of background clutter affects nectar bat use of flower odor and shape cues. *PLoS ONE* 10: e0136657.

Muchhala N, Thomson JD. 2010. Fur versus feathers: pollen delivery by bats and hummingbirds, and consequences for pollen production. *The American Naturalist* 175: 717–726.

van der Pijl L. 1961. Ecological aspects of flower evolution. II. Zoophilous flower classes. *Evolution* 15: 44–59.

R Development Core Team. 2022. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. [WWW document] URL http://www.R-project.org [accessed 3 July 2024].

Schnitzler HU, Moss CF, Denzinger A. 2003. From spatial orientation to food acquisition in echolocating bats. *Trends in Ecology & Evolution* 18: 386–394.

Simon R, Matt F, Santillan V, Tschapka M, Tuttle M, Halfwerk W. 2023. An ultrasound-absorbing inflorescence zone enhances echo-acoustic contrast of bat-pollinated cactus flowers. *Journal of Experimental Biology* 226: jeb245263.

Thiele J, Winter Y. 2005. Hierarchical strategy for relocating food targets in flower bats: spatial memory versus cue-directed search. *Animal Behaviour* 69: 315–327.

Tschapka M, von Helversen O. 2007. Phenology, nectar production and visitation behaviour of bats on the flowers of the bromeliad *Werauhia gladioliflora* in a Costa Rican lowland rain forest. *Journal of Tropical Ecology* **23**: 385–395.

Tschapka M, von Helversen O, Barthlott W. 1999. Bat pollination of *Weberocereus tunilla*, an epiphytic rain forest cactus with functional flagelliflory. *Plant Biology* **1**: 554–559.

Vickers NJ, Christensen TA, Baker TC, Hildebrand JG. 2001. Odour-plume dynamics influence the brain's olfactory code. *Nature* **410**: 466–470.

Vogel S. 1954. *Blütenbiologische typen als elemente der sippengliederung.* Jena, Germany: G. Fischer Verlag.

Vogel S. 1958. Fledermausblumen in Südamerika. *Plant Systematics and Evolution* **104**: 491–530.

Voigt CC, Kelm DH, Visser GH. 2006. Field metabolic rates of phytophagous bats: do pollination strategies of plants make life of nectar-feeders spin faster? *Journal of Comparative Physiology B* **176**: 213–222.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Dataset S1 Raw data from the flight cage experiments.

Fig. S1 An image of a *Burmeistera succulenta* flower showing the long stem and the complex background behind it typical of Neotropical cloud forests.

Fig. S2 An image of the experimental set-up for flight cage trials in a complex background.

Notes S1 The R script used for the statistical analyses, with results and comments.

Video S1 A video of a bat visiting a flower in the experiments.

Please note: Wiley is not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.