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Phenology, nectar production and visitation behaviour of bats on the flowers of the bromeliad *Werauhia gladioliflora* in a Costa Rican lowland rain forest

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Abstract: We studied the interaction between the bromeliad *Werauhia gladioliflora* and its flower visitors in the Caribbean lowland forest of Costa Rica, in order to quantify the mutual benefits to both partners. Over 6 y, the bromeliads flowered mainly between October and December; with an individual inflorescence flowering for an average of 34 d ($n = 233$ inflorescences). The bromeliad showed a flexible breeding system with autogamy occurring in addition to cross-pollination. Exclusive pollinators were small nectar-feeding bats (Phyllostomidae: Glossophaginae). The average volume of nectar produced per flower was 1.1 ml ($n = 25$ flowers). The main visitor was the bat *Glossophaga commissarisi*, which approached the flowers exclusively using hovering flight. Visitation by bats, measured by infrared light sensors, occurred throughout the night with an activity peak after midnight. Median hovering duration of the bats at the flowers was 320 ms ($n = 1246$ visits). Hourly mean of hovering duration was negatively correlated with hourly nectar secretion rate. The flower visitation behaviour of a bat over the night seems to be shaped by a combination of intrinsic physiological factors and by nectar availability. Size of both flowers and visitors make *Werauhia gladioliflora* a very accessible system for quantification of factors affecting evolution of bat–plant interactions.

Key Words: bat pollination, Bromeliaceae, chiropterophily, epiphyte, *Glossophaga commissarisi*, Glossophaginae, light-traps, nectar, Phyllostomidae, pollination

INTRODUCTION

In the Neotropics, specialized bat pollination systems have reached a high diversity and involve about 40 species of flower-visiting bat (Phyllostomidae: Glossophaginae) that largely depend on nectar (Dobat & Peikert-Holle 1985, Tschapka & Dressler 2002, von Helversen 1993). So far, most studies on bat-pollination have concentrated on the identification of pollinators or the verification of a predicted bat pollination syndrome (Baker 1970, Machado *et al.* 1998, Sazima & Sazima 1978, Sazima *et al.* 1989, 2003; Tschapka *et al.* 1999, Vogel 1958, 1969). Few studies have focused on the ecological aspects of resource use (Law 1995, Petit & Pors 1996, Sosa & Soriano 1993, Tschapka 2004). However, from a methodological point of view, plant pollination by bats is promising for quantitative ecological studies, since large

flowers and large pollinators allow access to parameters that are difficult to access in most other pollination systems. Quantification of these parameters, such as nectar secretion rates, phenology and bat visitation behaviour provide insights into the selective pressures experienced by both partners.

Since they are warm-blooded, nectar-feeding bats are subject to much harsher energetic selection than most other flower visitors (von Helversen & Winter 2003). Small bats have an unfavourable surface-to-volume ratio, consequently body heat loss is considerable and basic metabolic rates greatly surpass those of most other similar-sized mammals (von Helversen & Winter 2003). Additionally, energy investment in foraging is high, since most flowers contain only small amounts of nectar at a given time and consequently bats have to visit numerous flowers, which may involve travelling some 50–100 km per night (von Helversen & Reyer 1984, Winter 1999). Energetic considerations are therefore expected to play a major role in glossophagine foraging behaviour and

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consequently also in evolution of bat–plant interactions. On a community level, the energetic properties of the resources offered by flowers may determine resource use and the structure of nectar-feeding bat guilds (Tschapka 2004). However, a detailed quantitative monitoring of bat foraging behaviour together with nectar secretion patterns on food plants has been conducted only rarely (Gould 1978).

While looking for a system suitable for such a quantitative approach of bat pollination, we found in 1991 the bromeliad *Werauhia gladioliflora* in large numbers at the La Selva rain forest station in Costa Rica. Chiropterophily in bromeliads was first proposed by Porsch (1932), and the earliest field observations were conducted by Vogel (1969). Since then a number of observations on bat visits to bromeliads have been published (Araujo *et al.* 1994, Sazima *et al.* 1989, 1995). In a study in Bolivia, 7% of the bromeliads showed characteristics associated with bat pollination (Kessler & Krömer 2000). Cascante-Marin *et al.* (2005) studied the reproductive biology of *Werauhia gladioliflora* in a premontane tropical forest and reported small bats as visitors. However, long-term phenology, the significance of the bromeliads as a resource for the bats and vice versa, as well as temporal patterns of both nectar production and bat visiting behaviour have not been recorded to date. By simultaneously focusing on plant floral characteristics and bat behaviour we wanted to characterize the mutual adaptations of the bromeliad and its pollinators and asked the following questions: How is *Werauhia gladioliflora* adapted to pollination by bats and what are the main pollinating species? Does the plant represent an important resource for the bats? Building on these basic data and given the highly economic foraging behaviour of the bats (Winter & von Helversen 2001) we hypothesized that foraging behaviour of the bats should be significantly influenced by the plants' temporal nectar secretion pattern, so bats should visit flowers predominantly at times of high nectar production. On the other hand, given that bats are large and therefore expensive pollinators we hypothesized that the cost of large inflorescences and flowers and high amounts of nectar should be justified by a high dependence of the bromeliad on cross-pollination.

METHODS

Study site

Data were collected between 1991 and 1997 at La Selva Biological Station, Costa Rica. The study site is located on the Rio Puerto Viejo in the Atlantic lowland rain forest of Costa Rica (10°26'N, 83°59'W), 40–60 m asl and forest cover is tropical wet forest (Holdridge 1967). The climate

is humid with a precipitation of about 4000 mm y⁻¹ (Sanford *et al.* 1994). Observers were constantly present between August 1994 and March 1997 and during the main flowering seasons in the remaining years.

Flowering phenology

One hundred and twenty-five bromeliads were marked on a 2.1-ha clearing around the laboratory buildings of the station near the Puerto Viejo River and monitored for flowering between 25 October and 13 December, 1992. The concise inflorescence architecture and the strict temporal sequence of flowering on an inflorescence from the bottom up allowed each flower to be numbered and individually monitored. Each day we recorded for each inflorescence the number of the flower that had opened during the previous night. This numbering allowed us to track the development from individual flowers to fruits and served also as an index for the progression of flowering at an inflorescence. Low flower numbers corresponded to early flowering at the base of the inflorescence, whereas higher numbers indicated that the inflorescence was approaching the end of its flowering period. In 1992 and 1994–1996 phenology was recorded by periodically sampling a subset of the population; for 1991 and 1993 we extrapolated the flowering phenology using the flower numbers recorded on selected days and applying the flowering rate measured in 1992.

Pollination and fruiting success

About 6 wk after the main flowering period we recorded the presence or absence of fruit capsule development for each of the flowers in our sample. We calculated mean daily fruiting success i.e. the number of fruits set from the total number of flowers open on a single day, from the continuous observation period, while mean fruit set in the bromeliad population (fruits per flowers on a single inflorescence) was calculated from all inflorescences in the sample population.

Pollination experiments included the following treatments: (1) visitors excluded by covering the flowers with cloth bags, emasculated flowers; (2) visitors excluded; (3) artificial outcrossing, visitors excluded, emasculated flowers; (4) artificial self-pollination. Flowers were emasculated by removing the anthers before anthesis in the early evening. Artificial pollination in treatments (3) and (4) was done by rubbing a fresh anther from another plant against the stigma between 20h00 and 21h00. Pollen number produced per flower was determined running a subsample of a suspension of pollen grains from a flower through a cell counter (CASY1 Model TT, Schärfe System GmbH, Reutlingen, Germany).

Nectar measurements

Nectar was collected with a syringe (0.01-ml scale) throughout the night at 1-h intervals. Flowers were covered between sampling by cloth-bags to prevent animal visits. Nectar sugar concentration was measured using a field refractometer (Krüss, Hamburg, range 0–32%, weight/weight) to the nearest 0.1%. Total nectar volume per flower was calculated as the sum of the hourly values.

Bat captures

Bats were caught using mist nets set adjacent to flowering plants and across forest trails. Species were identified using an unpublished version of Timm & LaVal (1998), Webster (1993) and Emmons & Feer (1990). Pollen was collected from the bats immediately after capture by rubbing small pieces (*c.* $3 \times 3 \times 1.5$ mm) of fuchsin glycerine jelly (Beattie 1971) over the pelage of the animals. Samples were mounted on glass slides and pollen was identified under a light microscope (Olympus, $40\times$ – $400\times$) using a reference collection prepared from fresh flowers. Pollen occurrence was recorded on a presence/absence basis.

Recording of flower visits

We mounted infra-red light-traps (Sick WL-9-P13) to record bat visits with the light beam running parallel to the inflorescence in front of the flowers of *W. gladioliflora* (Figure 1, inset). Sensors were connected to a data-logger that recorded duration of each visit to the nearest 10 ms (Z80 microchip, design by A. Schmiedl, Erlangen). A second system based on an ATARI Portfolio microcomputer, was used for additional flowers, to record only the total number of visits. From the duration and pattern of light beam interruptions it was possible to identify each bat visit clearly, as interruptions caused by raindrops had extremely short durations, whereas long interruptions were caused by herbivorous insects (e.g. katydids). Additional visual observations of bat visits were made with a stereoscopic night vision device (Litton, 2nd generation).

RESULTS

General observations

In 1992 the clearing contained a population of 292 flowering bromeliads, most of which were epiphytic on scattered trees. Similar densities of plants were also observed on tree branches overhanging the river, as well as in glades adjacent to the river and similar places with high levels of light. The epiphytes were rarely found in the

upper canopy, and had in the forest an average ($\pm$ SD) growth height of 10.7 ± 6.1 m ($n=179$).

Phenology

The start of the main flowering period consistently occurred between the end of September and the beginning of October, and lasted until the middle or end of December. A small fraction of the population, less than 2% of the plants in the clearing, regularly flowered outside of the main flowering period in February or July (Figure 2a).

Inflorescence/flower morphology and anthesis

Inflorescences had a mean ($\pm$ SD) length of 41.4 ± 11.5 cm ($n=115$ inflorescences). Flowers were arranged in two rows (right/left) on the inflorescence but all opened in the same direction (secund orientation). Flowers opened from the bottom of the inflorescence up, alternating between the two rows. A single inflorescence produced an average of 27.2 flowers (SD = 7.0; $n=233$). The mean flowering rate was calculated as the number of flowers on an inflorescence divided by the observed flowering duration between first and last flower, and was 0.798 flowers d^{-1} (SD = 0.08; $n=55$ completely observed inflorescences). Applying this rate to the numbers of initiated flowers on all inflorescences, the average flowering duration was 34 d (SD = 8.8; $n=233$ inflorescences) per inflorescence.

Flowers started to open shortly before dusk, between 17h15 and 17h45, and wilted in the early hours of the following day after 4h00. The flowers of *W. gladioliflora* are greenish white with rigid petals and emit a distinct smell with components reminiscent of garlic. Six anthers and the style are positioned dorsally. The flowers had an entrance diameter of 17.1 ± 1.7 mm and a depth of 27.0 ± 2.2 mm ($n=26$). Flowers produced between 2.05×10^7 and 3.04×10^7 pollen grains ($n=3$ flowers). Most inflorescences opened only a single flower per night (96% of all observed flowering), however, occasionally (4%) we observed 2 consecutive flowers opening simultaneously.

Nectar production

Nectar production started when the flower opened around dusk, peaked at between 20h00 and 21h00 and then ceased after 4h00 in the early morning. Sugar concentration was around 17% until midnight and then decreased to 6% over the second half of the night (Figure 3). Mean nectar production per flower was 1120 ± 310 μ l per night ($n=124$). Nectar volume per flower (nvol) was negatively correlated to the

Figure 1. *Glossophaga commissarisi* visiting inflorescence of *Werauhia gladioliflora*. Stamens deposit pollen copiously on the forehead of the bat. Total length of the bat is c. 70 mm. (Photo taken in the field October 1995.) Inset: placement of infrared light traps for recording visits, cables to computer not shown.

respective flower number (fn) and positively correlated with the size of the inflorescence (sz = number of flowers per inflorescence): $nvol = 584 - 22.5 \times fn + 23.9 \times sz$ (multiple linear regression, $n = 66$, $R^2 = 0.48$, $P < 0.05$).

Fruiting success and pollination system

The average fruit-set per night in the population in 1992 was 0.61 fruits per flower ($SD = 0.09$, $n = 50$ d; 2755

flowers on 123 plants) (Figure 4). There was no significant correlation between fruit-set and the number of flowers opened each night in the population. Mean individual fruiting success per plant was 0.57 ($SD = 0.28$, $n = 123$ plants with 1916 fruits from 3325 flowers).

Flowers emasculated and shielded from animal visits did not produce any seeds ($n = 27$), while 83% of bagged flowers that were shielded but not emasculated developed a seed capsule ($n = 23$). Artificial cross-pollination

Figure 2. Flowering phenology of *Werauhia gladioliflora* at La Selva. Long-term phenology, based on monitoring subsets of the population between 1991 and 1996 (a). In the key to lines, numbers following years indicate the numbers of plants monitored in the respective year (= 100%). Large dotted lines indicate regular observation of a small number of flowering plants in February and July. Alternative phenology, based on pollen findings on flower-visiting bats between 1994 and 1997 (b).

resulted in a fruit set of 94% ($n=16$ flowers). Fruit capsules developed in 77% of the artificially self-pollinated flowers, indicating the potential for autogamy in *Werauhia gladioliflora*. Natural fruit set in the sample population was 58% ($n=3325$ flowers) and differed significantly from artificially cross-pollinated flowers and from flowers that were shielded from all visits ($\chi^2 = 53.6$; $df=4$; $P < 0.001$; plus post-hoc test for multiple comparisons of proportions, Zar 1996) (Table 1). Photos of flowers, taken at 60-min intervals during the night, showed no indication of an adaptive self-pollination mechanism achieved through the movement of floral parts.

Visitors

Observations using a night vision scope confirmed that small bats were the main visitors at the bromeliad flowers. In total 154 bats of four species were captured near flowering bromeliads. The most common bat species captured was *Glossophaga commissarisi* Gardner with 128 animals or 83% of the total captures. Less-

Table 1. Results from experiments on the reproductive system of *Werauhia gladioliflora*. Significant differences ($\chi^2 = 53.6$; $df=4$; $P < 0.001$; post-hoc test for multiple comparisons of proportions) are indicated by differing superscript letters. For comparison to the experimental treatments we report additionally the observed fruiting success in the whole population.

Treatment	Fruit-set (%)	N
Emasculated, no visitors permitted	0.0 ^c	27
No visitors	82.6 ^a	23
Artificial outcrossing	93.8 ^a	16
Artificial selfing	76.5 ^{ab}	17
Whole population	57.6 ^b	3325

frequent visitors were *Lichonycteris obscura* Thomas (14 = 9%), *Lonchophylla robusta* Miller (6 = 4%) and *Hylonycteris underwoodi* Thomas (6 = 4%), all of which belong to the specialized nectar-feeding bat subfamily Glossophaginae (Phyllostomidae). Pollen was frequently found in conspicuous yellow patches on the forehead of the bats, as expected from the position of the stamen and stigma (see also Figure 1). *Werauhia* pollen collected from flower-visiting bats provided an interesting comparison to

Figure 3. Nectar secretion patterns in *Werauhia gladioliflora*. Black dots indicate nectar production rate ($\mu\text{l h}^{-1}$); unfilled triangles represent sugar concentration. Data come from 25 flowers that were sampled hourly during the one-night life span. Hourly means (± 1 SD) are plotted at the mid-point of each sampling interval.

the observed flowering phenology (Figure 2a): *Werauhia* pollen was found on bats (mainly *G. commissarisi* and *Hylonycteris underwoodi*; $n = 504$) for most of the year and showed a small secondary peak in March (Figure 2b).

Although sphingid moths were not recorded visiting the flowers of *Werauhia gladioliflora*, we occasionally observed giant slow-flying moths, which were probably the noctuid moth *Otosema odorata* L. The only other regular nocturnal visitors were ants (mainly Ponerinae)

Figure 4. Flowering phenology and fruit set of *Werauhia gladioliflora*. Large black dots shows the daily numbers of flower produced by 123 plants in 1992, the dashed line shows the proportion of flowers that subsequently developed into fruits.

pilfering nectar, however, due to their small size and restricted movements these are unlikely to play an important role in pollination. We regularly observed hummingbirds, mainly the rufous-tailed hummingbird *Amazilia tzacatl* De la Llave, visiting opening buds in the evening and wilting flowers in the early morning.

Flower visitor behaviour

The number of bat visits recorded per flower ranged from 1 to 44 visits per night (median 15 visits, based on 1523 visits on 95 flowers). Interestingly, on three inflorescences that had no open flower on the respective night we recorded one, four and three bat visits.

Bats visited the flowers in brief hovering flights, starting around dusk with the first visits recorded before 18h00 (Figure 5a). Several times we recorded bats repeatedly visiting the same flower within a few seconds. Visiting rates peaked after midnight and ceased after 5h00 at the break of dawn. Median hovering duration was initially around 400 ms, dropped to 300 ms in the middle of the night and increased again after midnight to 600 ms or longer (Kruskal–Wallis Anova on ranks; $H = 64.5$; $df = 12$; $P < 0.001$; 1246 visits from 79 flowers). The median duration of all recorded visits was 320 ms (range 10–3690 ms) (Figure 5b).

Excluding the few very first and very last visits, median hourly hovering duration of bats correlated significantly with the mean hourly rate of nectar production of *Werauhia gladioliflora* (Figure 5c). Low rates of nectar production corresponded to longer hovering duration (Pearson correlation, $r = -0.614$; $P < 0.05$, $n = 11$, data from before 18h00 and after 5h00 with 15 and 5 visits, respectively, were excluded).

DISCUSSION

Structural adaptations of the inflorescence to bat pollination

Large flowers, high nectar production, nocturnal flowering and an unpleasant, garlic-like smell are common adaptations *Werauhia gladioliflora* shares with many chiropterophilous plants (Bestmann *et al.* 1997, Tschapka & Dressler 2002, Vogel 1969, von Helversen 1993). It is also noteworthy that all flowers in an inflorescence of *Werauhia gladioliflora* open in the same direction, in spite of initial bud formation on the inflorescence in two rows, facing opposite directions. This second flower orientation occurs on many chiropterophilous bromeliads (e.g. *V. kupperiana* Suess., *V. tonduziana* L. B. Sm., *V. ampla* L. B. Sm., *pers. obs.*; see also Benzing 2000) and might be helpful for bats, as it permits the animals to use the same approach route to feed every night. Glossophagine bats

have an excellent spatial memory (Thiele & Winter 2005, Winter & Stich 2005) and may repeatedly feed from a single inflorescence over its entire flowering period. The visits we recorded at inflorescences without open flowers indicate that bats may monitor inflorescences they have visited on previous nights. An inflorescence that can be approached every night along the same route reduces the orientation cost for the bat and may, therefore, increase the pollination success of the plant. Thus, second flower orientation in bromeliads could be an adaptation for pollination by bats.

Bats as a resource for *Werauhia*

In contradiction to our hypothesis, our experiments show clearly that, in spite of adaptations to chiropterophily, *W. gladioliflora* does not depend on bats and is capable of producing seeds autogamously. Self-pollination most likely occurs when flowers and sexual parts contract during wilting in the early morning (Cascante-Marin *et al.* 2005). Therefore, natural seed-set in the population probably occurs as a result of both cross-pollination and autogamy. However, even a few visits to a flower by a bat should be sufficient to reach saturation in cross-pollination, due to the large stamens of the bromeliad, and the large pollen transport capacity of the animals (Figure 1).

Our results from the tropical lowlands confirm the results of pollination experiments on *W. gladioliflora* in a premontane forest in Costa Rica (Cascante-Marin *et al.* 2005) and on the congener *W. sintenisii* from Puerto Rico (Lasso & Ackerman 2004) where cross-pollination did not significantly increase the pollination success of either species. Nevertheless, *W. gladioliflora* invests significant energy into attracting bats, by producing large inflorescences and flowers as well as producing large quantities of nectar and pollen. These costs might be justified by the added genetic variability of the offspring gained from cross-pollination using wide-ranging bats, compared to autogamy (Tschapka & Dressler 2002). Seedling establishment and survival in heterogeneous habitats might be supported by an increased genetic variability through added flexibility to substrate, light levels and humidity. Compared to the rain-forest interior, the main habitats of *Werauhia gladioliflora* along rivers are extremely dynamic due to air movement and water erosion processes and offer high microhabitat heterogeneity. *Werauhia gladioliflora* is also a successful colonizer of secondary habitats using its wind-dispersed seeds (Benzing 2000). Species colonizing heterogeneous habitats may profit from high genetic variability, but also from autogamy (Cascante-Marin *et al.* 2005).

Figure 5. Bat visitation behaviour at a population of *Werauhia gladioliflora*. Number of bat visits (a) and visit duration (b) per hour at flowers that were monitored by light-traps over the entire night. Data from 1246 visits at 79 flowers. Boxplots indicate 10th, 25th, 75th and 90th percentile; dots represent 5th and 95th percentile, respectively. The median is indicated by a solid, the mean by a dotted line. Mean nectar production rate versus mean hovering duration per hour (c). Numbers within the plot indicate the respective time intervals of the night.

Werauhia gladioliflora as a resource for the bats

The nectar produced by one flower equals 0.197 g sugar or 3.13 kJ (Tschapka 2004). During peak flowering, the population of 292 bromeliads in the 2.1-ha clearing therefore produced 914 kJ per night, which, assuming a daily energy expenditure (DEE) of 44.4 kJ for the 9-g *Glossophaga commissarisi* (von Helversen & Winter 2003), corresponds to the daily food requirements of 20–21 bats. *Glossophaga commissarisi* at La Selva preferably selected plants that provided high local energy density. High nectar production and the occurrence of plants in clumped populations make *Werauhia gladioliflora* a high-quality resource (Tschapka 2004). However, as the flowers, like those of other bromeliads (Araujo *et al.* 1994), are only available for part of the year only, the bats cannot depend solely on *Werauhia*. Consequently, at La Selva *Glossophaga commissarisi* used over 16 different species of nectar plants over the year and resorted to frugivory during a period of particularly low nectar availability, between March and August (Tschapka 2004, 2005).

We noted an interesting discrepancy in the observed flowering phenology of *W. gladioliflora* (Figure 2a) and the pollen records from the fur of nectar-feeding bats (Figure 2b). The first data set corresponds to flower availability, the second one shows actual flower use by bats. Pollen presence on bats proves availability of flowers, however, the number of bats carrying the pollen gives no indication of the actual number of plants flowering, as a single flower may be visited by several individual bats (Thomas 1988). Bats carried the pollen of *W. gladioliflora* not only during the main flowering season, between October and December, but to some extent over the entire year. A secondary peak in March corresponded roughly to the observations of very few flowering plant individuals (< 2%) within our phenology subset in February. The few flowers that were available at that time were visited by nearly 30% of the nectar-feeding bats at least once (Figure 2b), which indicates a high efficiency for flower location by glossophagine bats. This high efficiency probably also explains the early increase in bromeliad use before the observed main flowering period, as the bats immediately found the very first flowering inflorescences.

Bat visitation behaviour

Electronic monitoring showed that bats visit the flowers of *W. gladioliflora* throughout the night, with visitation frequency peaking after midnight. This continuous feeding on bromeliad flowers probably reflects both the significance of the resource as well as the high food requirements of the bats (von Helversen & Reyer 1984). Due to its high nectar volume and abundance *W.*

gladioliflora is one of the most profitable nectar resources in riverine habitats, which may be only matched by the liana *Mucuna holtonii* (Fabaceae) (Tschapka 2004). The increased visitation rate after midnight might be partly attributed to bats that had visited *Mucuna* in the first half of the night and were switching to an alternative food resource after the Fabaceae had stopped opening of new flowers (von Helversen & von Helversen 1999).

Some insectivorous bats leave the roost for only a few hours per night and, during this time, manage to obtain a sufficient amount of food (McCracken & Bradbury 1981). The physiological constraints of nectar-feeding, however, force small glossophagine bats to feed almost continuously throughout the night, with numerous foraging flights that alternate with periods of rest that allow the digestion of the consumed nectar. A bat the size of *G. commissarisi* needs to obtain roughly 100–150% of its body mass in nectar per night (von Helversen & Winter 2003). It is obvious that even under unlimited food conditions this amount could not be ingested within a short time, and even less when foraging on flowers that produce nectar only gradually. In this way, the food acquisition and processing limitations of the bat as well as nectar production pattern of food plants contribute to the continuous feeding behaviour of the bat throughout the night.

We could not confirm our initial hypothesis that bat visitation at flowers of *Werauhia gladioliflora* should peak with nectar secretion rates, as the maximum in visitation occurred several hours after maximum nectar production. However, the negative correlation between hourly nectar production rates and foraging investment in the form of hovering duration of the bats suggests that nectar availability does affect foraging behaviour of the bats, but in a less obvious way. Additionally, factors intrinsic to the bats may influence hovering duration: during the day glossophagine bats lose approximately 1–2 g of their body mass through a combination of fat mobilization and water loss (von Helversen 1995). Consequently, at the beginning of the night the animals are starving and dehydrated and during their first visits are investing slightly more hovering time into exploitation of the flowers (Figure 5c). After these first visits the most urgent needs are satisfied and bats continue to forage habitually. After midnight, however, nectar production rates decrease to about 50% of their maximum and the bats encounter lower nectar levels, so they have to visit more flowers to gain sufficient nectar, which contributes to the observed increase in visitation frequency. Greater visitation activity together with decreasing nectar production also increases the probability of bats encountering flowers emptied by other bats, so they leave quickly, which might explain the increased variability in hovering duration. Low nectar levels during the last hours of the night require bats to

spend a longer time probing the almost empty flowers with their extendible tongues, so hovering duration steadily increases. In conclusion, the visitation behaviour of a bat at the flowers of *Werauhia gladioliflora* seems to be influenced by physiological necessities, the mechanics of nectar uptake, and by temporal nectar production patterns of the chiropterophilous plants available in the habitat together with nectar consumption of other bat individuals.

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