Flower visitors of *Calathea lutea* (Marantaceae): The role of the hummingbird *Threnetes ruckeri*

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Most representatives of the pantropical monocot family Marantaceae have highly specialized flowers either adapted to bee or bird pollinators. However, bee-pollinated species are often reported to also be visited by birds, which may then act as co-pollinators or extract nectar without pollinating the flowers. A variety of flower visitors including orchid bees, butterflies and hummingbirds have been observed on *Calathea lutea*, a common Marantaceae species from Central and South America. While orchid bees are believed to be the main pollinators of *C. lutea*, butterflies have been observed to steal nectar without pollinating the flowers. The interactions with hummingbirds have not been studied in detail so far. In this study, we observed the flower-visiting behavior of the hummingbird *Threnetes ruckeri* (Trochilidae: Phaethornithinae) on *C. lutea* in southwestern Costa Rica. Our study focused on nectar removal by this bird species and on its potential role as pollinator. Nectar volume of unvisited flowers was measured at different times of day and compared to flowers that were visited by hummingbirds. We provide evidence that *T. ruckeri* does not pollinate these flowers, but acts as a nectar robber. The hummingbird pierces the sides of the corollae of fresh flowers with its beak and subsequently removes all nectar without touching the reproductive parts of the flowers.

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Vertreter der pantropisch verbreiteten einkeimblättrigen Familie Marantaceae haben spezialisierte Blüten, die entweder an bestimmte Bienen- oder Vogelarten angepasst sind. Bienenbestäubte Vertreter der Marantaceae werden jedoch oft von Vögeln besucht. Bisher ist unklar, ob Vögel als Co-Bestäuber agieren oder nur den Nektar der Blüten trinken. An *Calathea lutea*, einer häufigen Marantaceae aus Süd- und Mittelamerika, wurden Prachtbienen, Schmetterlinge und Kolibris als Besucher beschrieben. Prachtbienen gelten als Bestäuber und Schmetterlinge wurden als Nektardiebe von *C. lutea* klassifiziert. Ob Kolibiris zur Bestäubung der bienenbestäubten *C. lutea* beitragen, ist nach wie vor unklar. Wir beobachteten Blütenbesuche und Nektarentnahme des Kolibris *Threnetes ruckeri* (Trochilidae: Phaethornithinae) an *C. lutea* im südwestlichen Costa Rica. Die Nektarmenge von unbesuchten Blüten wurde zu verschiedenen Tageszeiten gemessen und mit der Nektarmenge von Kolibri besuchten Blüten verglichen. *T. ruckeri* kann als Bestäuber von *C. lutea* ausgeschlossen werden, da die Vögel mit ihrem Schnabel die Kronröhre der Blüten seitlich anstechen und den Nektar entnehmen, ohne mit den reproduktiven Blütenteilen in Kontakt zu kommen.

Keywords: Band-tailed Barbthroat, nectar robbery, nectar removal, nectar amount, pollination.

Introduction

The pantropical family Marantaceae comprises approximately 525 species that are abundant understory herbs in many tropical ecosystems (Andersson 1998, Costa 2006, Hammel et al. 2003, Poulsen & Balslev 1991). Interactions with pollinators are highly specialized within this family due to a unique pollination mechanism that involves secondary pollen presentation and an irreversible explosive style movement (Kennedy 1978). The style is

held under tension until a pollinator touches the trigger appendage of the style to release it. Once released, the style curls up explosively, moving the stigma forward to scrape off pollen from the pollinator, while the plant's own pollen is applied together with a sticky substance from the backside of the style to the same spot on the pollinator (for details see Classen-Bockhoff 1991, Jerominek & Classen-Bockhoff 2015, Kunze 1984, Endress 1996, Vogel 1984).

In most bee-pollinated Marantaceae species the pollen is pushed under the bee's tongue into the proboscidial fossa from where it cannot be removed by the animal (Andersson 1981, Ley & Classen-Bockhoff 2009). Large, long-proboscid orchid bees (Apidae: Euglossini) are the main pollinators in the Neotropics, while various short-proboscid bees are the principle pollinators in the Old World tropics (Dressler 1968, Kennedy 1978). Marantaceae are important nectar plants for bees due to the high amount of nectar and the long flowering period of each inflorescence, which can last for several weeks or even months. Euglossine bees are known to visit the same plants each day on a regular basis, following certain routes using a trap-lining strategy (Ackerman et al. 1982).

Notable exceptions of the bee-pollination syndrome are the ornithophilous taxa, e.g. three African species that are specialized in pollination by sunbirds (Ley & Classen-Bockhoff 2009) and the South American species *Calathea crocata* and *C. timothei*, both adapted to pollination by hummingbirds (Kennedy 1978, Nolasco et al. 2013). *C. schunkei* from the lowlands of Peru is also believed to be ornithophilous based on its red showy bracts and unusual floral morphology (Kennedy 2000). Adaptation in flower orientation and shape, stigma morphology as well as in the color of bracts were apparently necessary to ensure successful pollination by such long-beaked birds (Kennedy 1978, 2000, Ley & Classen-Bockhoff 2009).

The floral trigger mechanism of Marantaceae allows for distinction between possibly pollinated and clearly unpollinated flowers, and can also provide clues for the classification of visitors as potential pollinators or potential nectar thieves. For example, Davis (1987) noted that butterflies drink nectar but do not trigger the flowers. This has also been shown in extensive studies on butterflies visiting *Calathea lutea* and *C. crotalifera* in La Gamba, Costa Rica. Several species of Hesperiidae and one species of Riodinidae, *Eurybia lycisca*, were identified as nectar thieves because they extracted nectar without triggering the flower with their extremely long mouthparts (Bauder et al. 2013, 2011, 2015). The hummingbirds *Glaucus aeneus* and *Threnetes ruckeri* also visit the flowers of *C. crotalifera* without releasing the explosive style (Bauder et al. 2011). It has not yet been clarified whether they act as nectar thieves that steal nectar without damaging the flower, like the aforementioned butterflies, or as nectar robbers that actively make a hole in the flower to gain access to nectar. According to Stiles & Skutch (1989), *T. ruckeri* slits or pierces flowers of *Calathea* spp., and Kennedy (1978, 2000) suspected that hummingbirds visit bee-pollinated Marantaceae mainly to rob nectar by piercing flowers and to take up water from the phytotelmata which are formed by the bracts subtending the flowers. However, in another study conducted in La Gamba, Costa Rica (Classen-Bockhoff & Heller 2008) on *C. lutea* and *C. crotalifera* (*C. platystachia* in that study), hummingbirds were also seen triggering flowers during nectar drinking and were therefore assumed to occasionally co-pollinate these plant species in addition to the orchid bee pollinators. A similar situation was found in *Saranthe klotzschi-*

ana from Brasil and in the Costa Rican *Thalia geniculata* (Davis 1987, Locatelli et al. 2004).

While the antagonistic role of flower-visiting butterflies on *C. crotalifera* and *C. lutea* is clearly understood and well documented, the role of hummingbirds has not been investigated in detail (Bauder et al. 2011, 2015, Classen-Bockhoff & Heller 2008, Kennedy 2000). In this study, we focused on the interaction of the hummingbird *T. ruckeri* with *C. lutea* flowers in southwestern Costa Rica. We measured the nectar availability and sugar concentration in flowers at different times of a day and documented the hummingbirds' nectar removal in order to clarify their potential role as mutualistic pollinators or antagonistic nectar thieves/robbers.

Materials and Methods

Study area, study sites and time

The study was conducted at the Tropical Field Station La Gamba and in the nearby Piedras Blancas National Park in southwestern Costa Rica. Fieldwork was conducted during the dry season (January - March) of 2011 and 2019.

Three sites with *C. lutea* were studied. Site 1 is located at the border of the P.N. Piedras Blancas. This site has an area of approximately 1000 m² and is densely covered with *Dieffenbachia aurantiaca* and > 100 individuals of *C. lutea.* Site 2 consists of approximately 50 individuals of *C. lutea*, which are situated along a small stream in the garden of the research station. This site is smaller than site 1 and of open habitat type. Site 3 consists of approximately 50 individuals growing along the 100 m long main trail through the research station and about the same distance along the road to the town of La Gamba. The distance between these sites is in the range of 50–200 m (1–2: 150 m, 1–3: 200 m, 2–3: 50 m).

Study plants, inflorescences and flowers

Plant, inflorescence and flower morphology as well as descriptions of anthesis of *C. lutea* are given in detail elsewhere (Bauder et al. 2015, Classen-Bockhoff & Heller 2008, Düster et al. 2018, Hammel et al. 2003) and are summarized here.

C. lutea grows to a height of 2–4 m in populations of variable size, often along streams or in open areas that are fully exposed to the sun (Hammel et al. 2003). The large inflorescences are located 1–3 m above the ground and are composed of several approx. 20 cm long partial inflorescences ('florescences'), each bearing a total of approx. 100 flowers. The flowers emerge from phytotelmata (water filled compartments) that are formed by stiff reddish bracts. Each bract holds five to seven pairs of flowers that develop successively, so that each florescence holds an average of three open flowers per day. A florescence may flower for several months. Flower buds are only visible on the evening before anthesis, which usually starts around 5:00 in the morning. The flowers last for a few hours and start to wilt at around 10:00 of the same morning, before falling to the ground at around 18:00 of the same day (Classen-Bockhoff & Heller 2008). The perianth is rather inconspicuous and has a similar brown-reddish colour as the bracts. Once the perianth opens, the modified yellow staminodes and the style that form the trigger mechanism are presented.

The length of the floral tube, formed by the staminodes, is about 31 mm (Bauder et al. 2015). Each flower contains approx. 12 µl of nectar with a sugar concentration of 40 % (Düster et al. 2018, Ruppel & Morlock 2015).

Hummingbird flower visitation and nectar extraction

Flowering individuals within two sites (Site 1 and 2) were observed by sitting in front of a few chosen inflorescences for several hours per day (see below). We recorded all hummingbirds visiting inflorescences, noted the daytime of each visitation and documented their feeding habits by photographs and video recordings using digital cameras (Canon Eos 60D, Canon Ixus 970 IS, Panasonic Lumix DMC-FZ200EG9, Sony HDR-PJ10). The observations took place in February 2011 (5 days) and February 2019 (3 days).

We paid special attention to the way the birds inserted their beaks into flowers and the condition of a flower before and after visitation, i.e., whether the trigger mechanism was released or not. Two *C. lutea* sites were observed in 2011. Site 1 was observed for three days, and site 2 for two days. Observations took place three times per day, during a 60-minute period in the early morning (6:00–7:00) and one 90-minute period each during late morning (8:00–9:30) and late afternoon (15:00–16:30). Identification of hummingbirds was undertaken by bird identification books (Garrigues & Dean 2013, Stiles & Skutch 1989).

In 2019, we paid special attention to nectar extraction by hummingbirds at site 1. To test if flowers visited by hummingbirds contained smaller volumes of nectar than unvisited flowers, and whether hummingbirds pierced the perianth to access the nectar, we studied the floral tube and nectar level in flowers that had been visited by hummingbirds as well as unvisited control flowers. For this purpose, we removed all flowers from 21 florescences of two different individuals from site 1 in the evenings on three successive days and bagged these florescences with fine mesh nylon gauze. During the next days, we unbagged all the florescences at 06:00, 08:00, 10:00, 14:00 and 16:00 for 45 minutes at any one time allowing for animal visits. All flowers visited by a hummingbird were removed immediately after visits for morphological investigation and nectar analyses. Additionally, the same number of unvisited flowers from the same individual was removed to perform the same morphological and nectar analyses. Both types of flowers were analyzed for marks of nectar robbery (i.e., slits in the floral tube) using a stereo microscope (Leica-EZ4). The nectar volume was determined based on the nectar level in the floral tube by observing it against a light source. This method was tested prior to the experiment on eleven randomly selected flowers from which we measured the level of nectar in the floral tube and extracted it with capillaries to determine the volume. Given that nectar level was a good predictor of volume, as shown by a correlation analysis (Pearson $r = 0.84$, $p < 0.01$, $n = 11$ flowers), we used the linear fit function for all further analyses to determine the nectar amount.

Nectar volumes of hummingbird-visited flowers and unvisited control flowers were compared by a t-test for dependent samples (Statistica 12; StatSoft Inc. 2013) after tests for normality (Kolmogorov-Smirnov) and homogeneity of variances (Hartley).

Frequency of hummingbird nectar extraction and influence on nectar volume

To determine the frequency of nectar extraction by hummingbirds, 60 unbagged flowers were randomly collected in 2019 in the afternoon of February 25th from sites 1 (30 flowers) and 3 (30 flowers). All were checked for penetration marks and nectar volume. In addition to the vertical marks left behind by hummingbirds, we also detected marks with a different shape (see results) and thus classified the flowers into the categories 'hummingbird damage', 'other damage' and 'no damage'.

Nectar volumes of the different classes were analyzed by a Kruskal-Wallis ANOVA followed by a Tukey-HSD post hoc test for non-parametric data (Statistica 12; StatSoft Inc. 2013).

Number of open flowers, nectar volume and nectar concentration over the course of a day

Four plant individuals from site 1 and six individuals from site 3 were randomly selected to determine the number of open flowers, nectar volume, and nectar concentration over the course of a day. Several florescences (5–20, depending on availability) of each individual were bagged with fine mesh nylon gauze to exclude floral visitors. At 16:30 of three successive days, all open flowers within the bags were removed. During the following mornings, the number of open flowers available in the bagged florescences was determined at 06:00, 08:00, 10:00, 14:00 and 16:00 to learn about the number of flowers available at a certain point in time. In addition, one bagged flower per individual (n = 10 individuals) and time was randomly selected to measure the nectar properties (if available, 5 flowers per individual and day; 15 flowers during the three days of the experiments per individual; due to a sometimes small number of flowers available per individual, only 126 and not 150 flowers were sampled in total). Nectar concentration was measured by removing the ovary of each flower and pressing a droplet of nectar on an Eclipse handheld refractometer (0–50 Brix; Bellingham + Stanley Ltd.) and the nectar volume was determined using the method described above in section 'Hummingbird flower visitation and nectar extraction'.

PERMANOVA analyses (time as fixed factor; 10000 permutations) based on pairwise Euclidean distances among the nectar properties / flower counts, were calculated in Primer 7.0.13 with the add-on package Permanova+1 (Anderson et al. 2008, Clarke & Gorley 2015) to test for differences in the nectar volume of flowers, nectar concentration and the number of available flowers at different times of day. Given that plant individuals were repeatedly sampled, we included individual as a random factor in the analyses.

Complete names of plant and animal species treated or mentioned in the text

Plants: *Dieffenbachia aurantiaca* Engl., *Calathea crocata* E. Morren & Joriss., *C. crotalifera* S.Watson, *C. lutea* (Aubl.) Schult., *C. platystachya* Standl. & L.O.Williams, *C. schunkei* H.A.Kenn., *C. timothei* H.A.Kenn., *Heliconia stilesii* J.W.Kress, *Saranthe klotzschiana* Eichl., *Thalia geniculata* L.

Animals: *Amazilia tzacatl* (De la Llave, 1833), *Eulaema cingulata* (Fabricius, 1804), *Eufriesea surinamensis* (Linnaeus, 1758), *Eurybia lycisca* Westwood, 1851, *Glaucus aeneus* Law-

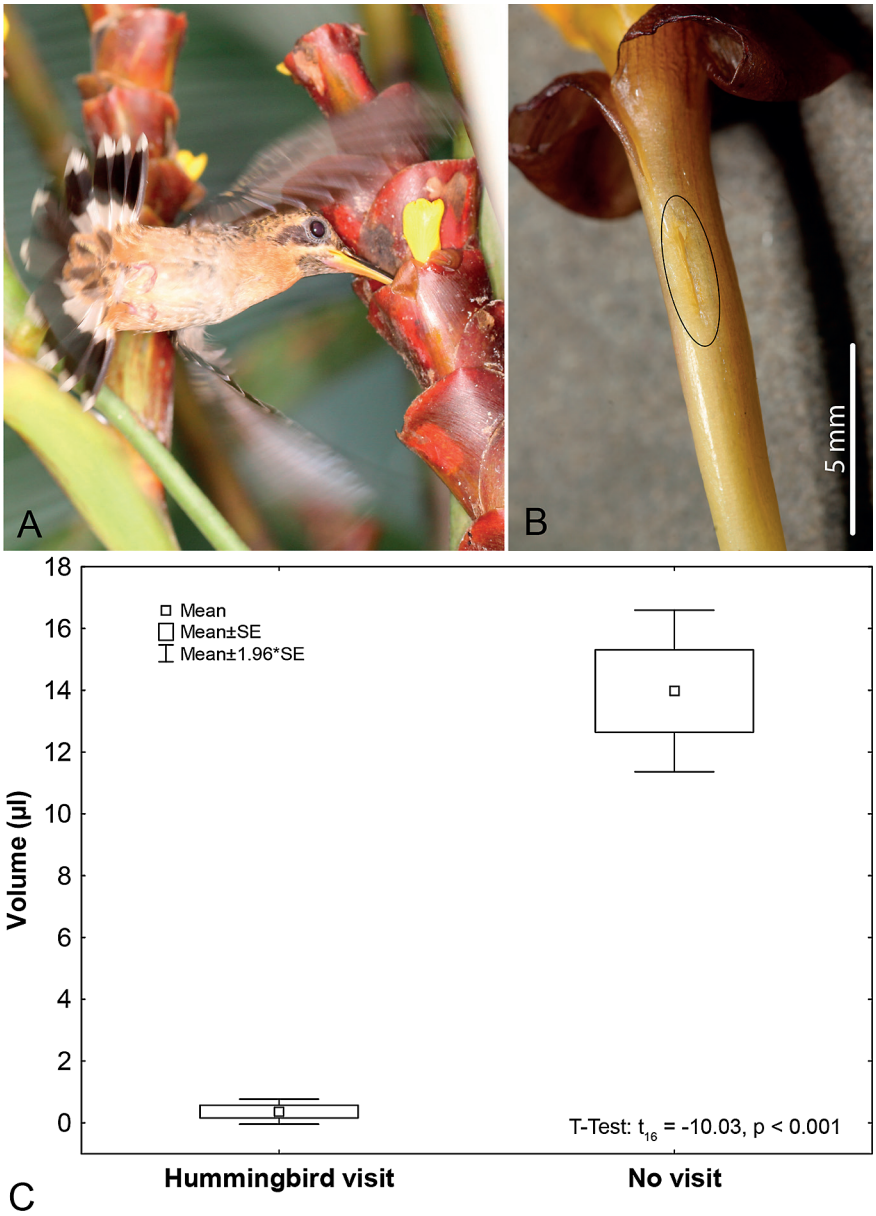

Fig. 1: A: The hummingbird *Threnetes ruckeri* piercing a flower of *Calathea lutea* from the side (Photo: Etl). B: A characteristic vertical slit in the floral tube of the flower left by the beak of *T. ruckeri* (Photo: Etl). C: Nectar volume of flowers of *C. lutea* visited by *T. ruckeri* (n = 26 flowers) and unvisited flowers (n = 26 flowers). Flowers visited by *T. ruckeri* contained less nectar than unvisited control flowers. – Abb. 1: A: Der Kolibri *Threnetes ruckeri* sticht seitlich in eine Blüte von *Calathea lutea* (Photo: Etl). B: Die charakteristische vertikale Einstichstelle in der Kronröhre einer Blüte von *C. lutea*, verursacht durch den Schnabel von *T. ruckeri* (Photo: Etl). C: Nektarmenge von *C. lutea* Blüten die von *T. ruckeri* besucht wurden (n = 26 Blüten) und unbesuchte Blüten (n = 26 Blüten). Blüten die von *T. ruckeri* besucht wurden enthielten weniger Nektar als unbesuchte Kontrollblüten.

rence, 1868, *Phaetornis longirostris* (Delattre, 1843) [formerly *P. superciliosus* (Linnaeus, 1766)], *Threnetes ruckeri* (Bourcier, 1847).

Results

Hummingbird flower visitation and nectar extraction

Threnetes ruckeri, a common hummingbird of the region, was the only hummingbird species documented during our observations. Observations over a period of five days in 2011 showed 25 visitations of *T. ruckeri* on inflorescences of *C. lutea*. The birds strictly visited flowers from the side (Fig. 1A, online video: https://youtu.be/cCqA2tYEUhQ) and pierced the flowers in the middle of the corolla (Fig. 1B). They pressed their beak deep into the floral tube without triggering the pollination mechanism. Visitations occurred mainly in the afternoon but also during the morning (Fig. 2). Typically, the birds consecutively visited several flowers (both triggered and untriggered ones) from different florescences. Sometimes they also stuck their beak into a phytotelmata without any flowers and poked around in it.

During the three days of observations in 2019, eleven visitations by *T. ruckeri* were documented in which the birds visited a total of 26 flowers. We noted a vertical penetration mark on the side of the floral tube at about 1.5 cm below the top of the flower in all visited flowers (Fig. 1B), whereas control flowers had no penetration marks. The flowers visited by hummingbirds contained less than 1 µl of nectar, whereas unvisited flowers contained around 14 µl (Fig. 1C).

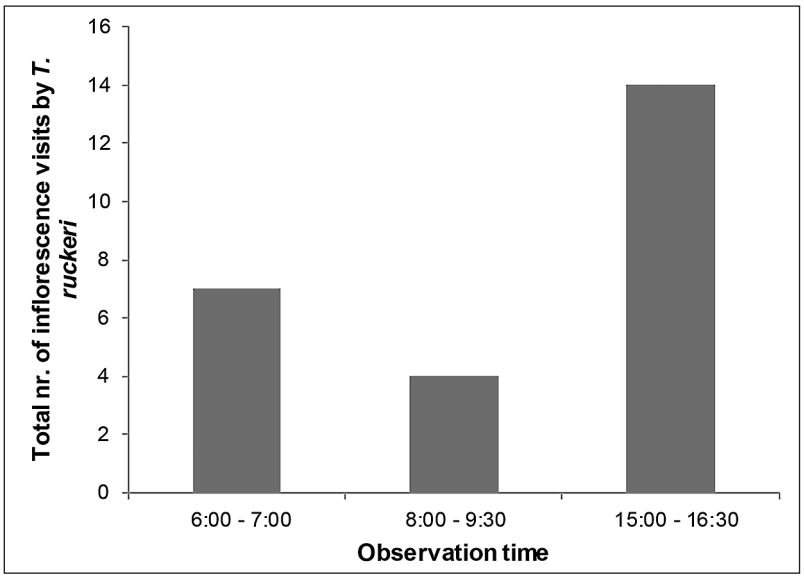

Fig. 2: Total number of inflorescence visits (to flowers and phytotelmata of *Calathea lutea*) by *Threnetes ruckeri* over five days of observations during specific time intervals. Depending on time of day, between four and 14 visitations were observed per time interval. – Abb. 2: Anzahl von Infloreszenzbesuchen (zu Blüten und Phytotelmata von *Calathea lutea*) durch *Threnetes ruckeri* innerhalb bestimmter Zeitintervalle während fünf Beobachtungstagen. Je nach Tageszeit wurden zwischen vier und 14 Besuche beobachtet.

Frequency of hummingbird nectar extraction and influence on nectar volume

At site 1, flowers with 'no damage' constituted the largest portion (53.3 %) of randomly collected flowers, and with 13 µl they also contained the highest mean nectar volume, followed by 'hummingbird damage' with 33.3 % and a mean nectar volume of 4 µl. Flowers with 'other damage', i.e. round cuts along the floral tube caused by other, unknown visitors, were the least frequent (13.3 %), with the mean nectar volume being similar to 'hummingbird damage' flowers. The flowers collected from site 3 showed no signs of hummingbird damage. Half of the flowers had 'no damage', the other half had 'other damage'; intact flowers contained a higher mean nectar volume (9 µl) compared to the 'other damage' flowers (4 µl). Overall (pooled among sites), flowers with no damage had a median of eight times more nectar than flowers with damage by hummingbirds or other unidentified visitors (Fig. 3).

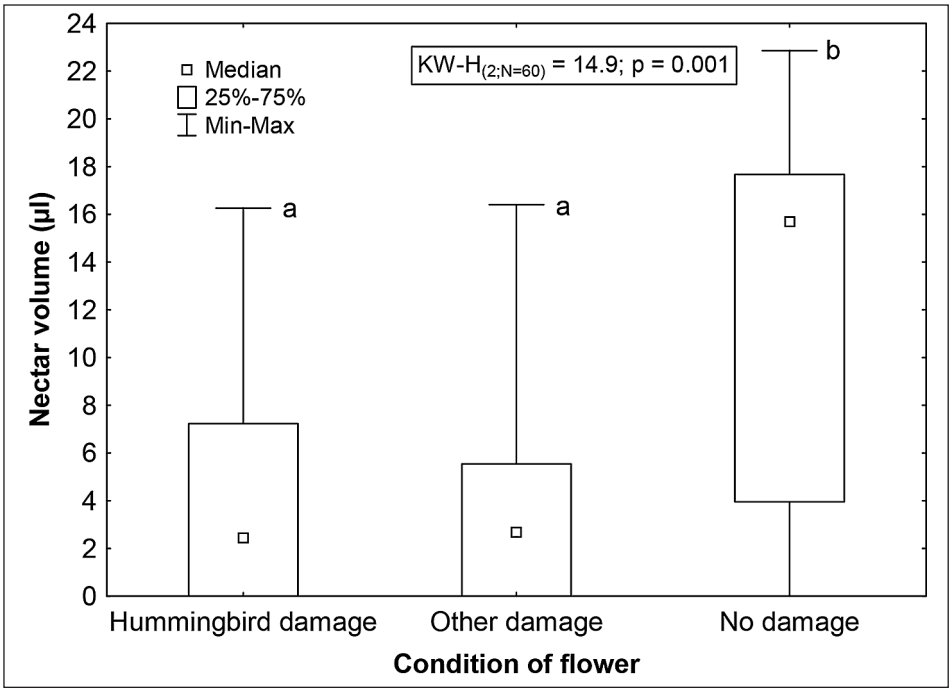

Fig. 3: Nectar volumes of differently damaged and undamaged flowers (n = 60) of *Calathea lutea*. Undamaged flowers contained higher nectar volumes than damaged flowers independent of the kind of damage. Different letters (a, b) indicate significant differences. – Abb. 3: Nektarmenge von unterschiedlich beschädigten und unbeschädigten Blüten (n = 60) von *Calathea lutea*. Unbeschädigte Blüten enthielten mehr Nektar als beschädigte Blüten, unabhängig von der Art der Beschädigung. Verschiedene Buchstaben (a, b) geben signifikante Unterschiede an.

Number of open flowers, nectar volume and nectar concentration over a day

The number of anthetic flowers per time varied over the day. At 6:00 a.m. a smaller number (76 % of the maximum number of flowers open per time) of flowers was available than later during the day (80 % - 84 %). The number of open flowers was constant from 8:00 a.m. onwards (Fig. 4).

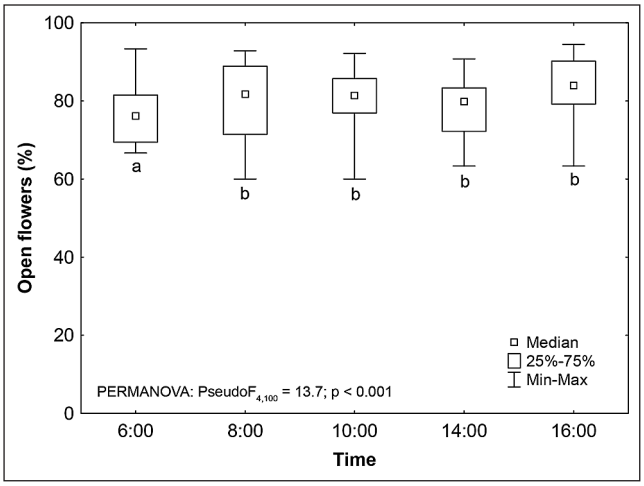

Fig. 4: Percentage of open flowers of *Calathea lutea* at different times of a day standardized using the maximum flower number per time category per day and individual. Mean values of the replicate measurements (over three days) per individual and time category were used for plotting purposes; statistical analyses were based on the original count data. At 6:00 a smaller number of flowers was available than later during the day. Time categories with different letters (a, b) differ among each other according to post-hoc analyses. – Abb. 4: Prozentzahl offener Blüten von *Calathea lutea* zu unterschiedlichen Tageszeiten, standardisiert unter Verwendung der maximalen Anzahl an Blüten je Zeiteinheit pro Tag und Individuum. Mittelwerte der Replikate (Messungen über drei Tage) pro Individuum und Zeiteinheit wurden geplottet, statistische Analysen basieren auf den ursprünglichen Zählungen. Um 6:00 waren weniger Blüten vorhanden als zu den späteren Messungen. Zeitkategorien mit verschiedenen Buchstaben (a, b) unterscheiden sich laut post-hoc Analyse voneinander.

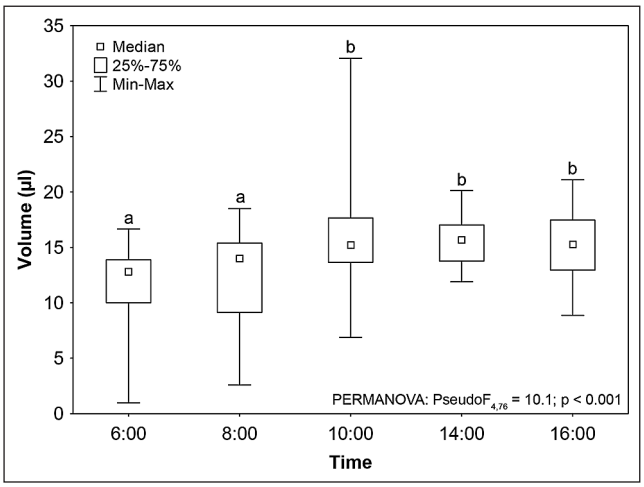

Fig. 5: Nectar volumes of bagged flowers (n = 126 flowers) of *Calathea lutea* measured at different times of day. The nectar volume was smaller in the early morning hours than later during the day. Different letters (a, b) indicate significant differences in volume. – Abb. 5: Nektarmengen von eingepackten Blüten (n = 126 Blüten) von *Calathea lutea* zu verschiedenen Tageszeiten. Die Nektarmenge war am frühen Morgen geringer als zu den späteren Messungen. Signifikante Unterschiede sind durch unterschiedliche Buchstaben (a, b) gekennzeichnet.

We found differences in the nectar volume of flowers over the day (Fig. 5), whereas nectar concentration did not differ over the day (median nectar concentration = 35 % and 40 %, n = 126 flowers; Fig. 6). The median nectar volume of flowers measured at 6:00 and 8:00 was 13 µl and thus significantly lower than the nectar volumes measured later in the day (15 µl; see Fig. 5; n = 126 flowers).

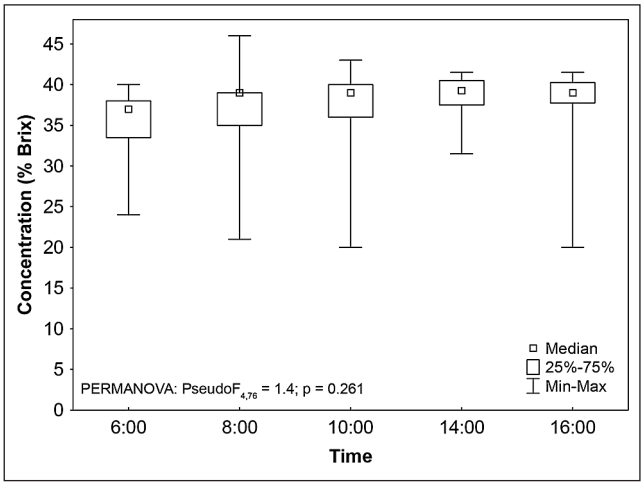

Fig. 6: Nectar concentrations of bagged flowers (n = 126 flowers) of *Calathea lutea* measured at different times of day. Concentration did not change significantly in the course of the day. – Abb. 6: Nektarkonzentrationen von eingepackten Blüten (n = 126 Blüten) von *Calathea lutea*, gemessen zu verschiedenen Tageszeiten. Es gab keine signifikanten Änderungen der Nektarkonzentration im Tagesverlauf.

Discussion

Our data show that individuals of the hummingbird species *Threnetes ruckeri* regularly and repeatedly visit inflorescences of *C. lutea* to pierce flowers and remove most of the nectar available in the flowers without touching reproductive parts of the flower, thus making them nectar robbers. Nectar robbery by hummingbirds is a widespread phenomenon across several families of Angiosperms in the Neotropics, especially on long-tubed flowers (Boehm 2018, Lara & Ornelas 2001). Darwin (1876) mentioned short-billed hummingbirds as nectar robbers that pierce the base of deep corollas to access nectar. Hummingbirds can rob from flowers that are pollinated by other hummingbirds (Lara & Ornelas 2001) or from insect-pollinated flowers, as shown in this study.

Though we provide evidence that *T. ruckeri* acted as a nectar robber, this does not mean that all hummingbirds that have been reported to visit *C. lutea* behave in this way. The two hummingbird species *Phaetornis longirostris* (former *P. superciliosus*) and *Amazilia tzacatl* were reported to insert their beak into the floral tube of several flowers of *C. lutea* to drink nectar while sometimes triggering the flowers (Classen-Bockhoff & Heller 2008). Their beak might be better suited for insertion into the corolla compared to the beak of *T. ruckeri*. However, it is unclear if pollen is deposited onto the beaks of these species and finally onto the stigmas of *C. lutea*. It is also uncertain whether *T. ruckeri* acts as a legitimate pollinator of other plant species in the area, or if nectar robbery is its preferred way

of nectar extraction in all visited species. Gill (1987) reported on nectar thievery by *T. ruckeri* at flowers of *Heliconia stilesii* on the nearby Osa Peninsula in Costa Rica.

As we observed hummingbirds visiting phytotelmata with flowers and without flowers (see also Classen-Bockhoff & Heller 2008, Kennedy 1978), we assume that they occasionally also drink water from the phytotelmata, and likely also feed on various unidentified arthropod larvae inside the liquid (Etl et al. unpub. data). As many old flower parts become macerated within the phytotelmata and likely still contain leftover nectar from pierced flowers, we suppose that the liquid inside the phytotelmata also contains sugar. However, sugar was not evidenced by preliminary measurements using the refractometer described above. Further investigations of the chemical content of the liquid might reveal other nutrients that are possibly taken up by the hummingbirds.

Nectar removal by nectar thieves and robbers might affect reproduction of *C. lutea* species, as the amount left for orchid bee pollinators is reduced (Bauder et al. 2015). How this influences the behavior of bees, and if they visit more or less flowers on an inflorescence than usual on their foraging trips has not been clarified so far and could have negative or positive effects on plant fitness (Burkle et al. 2007, Irwin et al. 2010, Maloof & Inouye 2000). Bees might avoid patches where *T. ruckeri* and long-proboscid butterflies are abundant and exclude such patches from their daily routes.

The bee species *Eulaema cingulata* and *Eufriesea surinamensis* recognize and actively open the flowers of *C. lutea* in late bud stage (Etl unpub. data), while they are still covered by brownish petals. Given that the trigger mechanism already works at this floral stage and pollen is already available, these visitations can also lead to pollination. This behavior might be a response to high rates of nectar robbery by hummingbirds and nectar thievery by butterflies. Such early stage flowers might have a higher probability of still holding nectar. As the flowers are still closed and inconspicuous during the bud stage, butterflies most likely cannot insert their proboscises. It remains unclear if hummingbirds visit such flowers. Their method of flower-piercing (sideways) would also allow nectar to be extracted from closed flowers. On the other hand, hummingbird visitation was highest in the afternoon, which might be a strategy to decrease nectar competition with bees in the morning, the time of highest bee activity on flowers of *C. lutea* (Etl unpub. data). As shown in this study, open flowers of *C. lutea* are also available in the afternoon and nectar volume is slightly higher at that time, which could be another advantage for *T. ruckeri*.

Conclusion

Based on its abundance in the region and the amount of described interactions, *C. lutea* is of great importance for various butterfly, bee and hummingbird species looking for nectar (Bauder et al. 2015, Classen-Bockhoff & Heller 2008). As hummingbirds of the species *T. ruckeri* did not make contact with the style when removing nectar by flower piercing, they are classified as nectar robbers. These nectar robbers as well as nectar thieves (butterflies) visit the flowers frequently, and extract considerable amounts of nectar (Bauder et al. 2015, this study). They likely have a strong influence on the behavior of legitimate pollinators and on plant reproduction. Their role in the evolution of plant-pollinator mutualisms may be underestimated (Irwin et al. 2010) as floral traits are under selective pressures by both mutualists and antagonists (Ehrlén et al. 2012, Irwin et al. 2001, 2004, Knauer et al. 2018, Schiestl 2015).

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