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Article

Sunbirds' tendency to hover: the roles of energetic rewards, inflorescence architecture and rain

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Although the Old World sunbirds are generally considered to be an ecological analogue of the New World hummingbirds, it is commonly believed that in contrast to hummingbirds, sunbirds perch while feeding. Nevertheless, recent studies have shown that Old World nectarivores hover while feeding more frequently than previously thought, and some Old World plants seem to have adapted to hovering bird pollinators. To reveal the importance of sunbird foraging behavior in nectar acquisition and to test whether this behavior is determined by plant architecture and rain intensity, we focused on the specialized West African pollination system of *Impatiens sakeriana* and its two major pollinators, the Cameroon sunbird *Cyanomitra oritis* and the northern double-collared sunbird *Cinnyris reichenowi*. *C. oritis* hovered more often than *C. reichenowi* while feeding on flowers, although both species were observed hovering regularly. For both species, hovering reduced the feeding time, but this reduction and the consequent estimated changes in energetic intake were species-specific. We found that both floral pedicel and peduncle length, as well as precipitation, negatively affected the probability of *C. reichenowi* hovering but did not have any significant effect on the behavior of *C. oritis*. Our study demonstrates that hovering behavior is common in the studied sunbird taxa and that plant architecture and environmental factors can influence sunbird foraging behavior. Nevertheless, the extent of hovering versus perching behavior, as well as the effects of biotic and abiotic factors, is species-specific.

Keywords: *Cinnyris reichenowi*, *Cyanomitra oritis*, foraging behavior, hovering, *Impatiens sakeriana*, Mount Cameroon

Introduction

Nectar serves as a reward and forms an essential component of the diet for more than 900 bird species (Krauss et al. 2017). Specialized nectarivorous birds are restricted to only a few lineages, with the majority belonging to three families: hummingbirds (Trochilidae), sunbirds and spiderhunters (Nectariniidae) and honeyeaters (Meliphagidae; Stiles 1981).

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Nectar-feeding birds exhibit various common physiological and morphological adaptations related to their diet and associated lifestyle (Stiles 1981). However, some traits are unique to a particular bird family, with the most famous example being the insect-like whirring flight typically performed by hummingbirds while feeding on flowers (Westerkamp 1990). This type of motion is possible thanks to an extraordinary rotation in the wrist together with a reduction in the relative size of the proximal skeletal wing elements, large pectoral muscles and other morphological and physiological alterations (Warrick et al. 2005, Hedrick et al. 2012) and allows hummingbirds to continuously hover for tens of minutes (Lasiewski 1963).

For decades, it has been thought that these adaptations restrict hummingbirds to sustained hovering, i.e. active flight in a specific location in windless air, without pauses in flapping during which the wings are held either bound to the body or extended for a period corresponding to one or more wingbeat cycles (Zimmer 1943, Tobalske 2010) and that this is reflected in specific evolutionary trajectories of bird–pollinated plants across continents. This idea was also supported by many studies, mainly from South Africa, showing Old World plants facilitating the perching of birds during flower visits (De Waal et al. 2012). Nevertheless, Miller (1985) observed that hovering is not necessarily the preferred mode of hummingbird foraging behavior, and Westerkamp (1990) noted that sunbirds can also hover. Consequently, they suggested that plant architecture rather than bird hovering ability underlies bird foraging behavior. Moreover, Westerkamp (1990) noted that some plants, where solitary flowers (or inflorescences where only one flower opens on a given day) are oriented towards free space, easily accessible to flying animals and without perches nearby (traits displayed by many hummingbird–pollinated plants) can even be found in Africa or Asia.

New empirical insights into this topic were produced by a few recent studies. First, Geerts and Pauw (2009) described the behavior of three sunbird species visiting invasive South American tree tobacco *Nicotiana glauca* in South Africa. All observed sunbird species showed a hovering ability while feeding, and the malachite sunbird *Nectariniia famosa* hovered during 80% of all visits. Second, Janeček et al. (2011) demonstrated that the Cameroonian *Impatiens sakeriana*, which has a long peduncle and is native in West Africa, is pollinated by two regularly hovering sunbird species. Furthermore, Wester (2013) observed that two sunbird species hover regularly over flowers of South African *Salvia* and *Lycium* species. Additionally, Wester (2014) compiled available information concerning sunbird and honeyeater foraging behavior, and the results indicated that 46 species of sunbirds and 15 species of honeyeater displayed hovering behavior while feeding. Similar to other passerines (Norberg 1975, Tobalske et al. 1999), sunbirds were seen hovering usually for several seconds. The longest reported hovering performance of a sunbird (*N. famosa*) lasted for approximately 30 s (Geerts and Pauw 2009).

According to the newest observations, some sunbirds prefer to hover while feeding even when a suitable perch is available (Padyšáková and Janeček 2016). This finding is in concordance with an alternative explanation for hovering performance proposed by Pyke (1981), who claimed that the behavior of pollinators might be explained simply by rules known from the optimal foraging theory. In his opinion, there are situations in which hovering is beneficial for birds, as it enables birds to visit more flowers and thus increases their energy intake in time. His suggestion is supported by the finding that hovering flower visits are generally shorter than perching flower visits (Padyšáková and Janeček 2016).

In addition to plant characteristics and bird anatomical (or physiological) constraints, bird behavior can be affected by climatic conditions, including precipitation (González et al. 2009). Due to their high metabolic rate (Lasiewski 1963, Prinzinger et al. 1989), nectarivorous birds often keep feeding on flowers under moderate or even heavy rain. This is especially true in areas with a tropical wet (or monsoon) climate, where the vast majority of precipitation falls during a few months.

Naturally, flying in rain represents a major challenge, mainly for two reasons. The first is wetting of the plumage. Although bird feathers (and especially feathers of terrestrial birds) are highly hydrophobic (Rijke and Jesser 2011) and under light precipitation should protect the animal sufficiently, their water-repellency is limited, and heavier rain may negatively affect the animal, for example by inducing elevated thermal losses. Moreover, most sunbirds as well as hummingbirds are to a large degree covered by iridescent plumage, whose modified feather structure decreases hydrophobicity (Eliason and Shawkey 2011). The second reason is mechanical. Water loads remaining on the bird's body increase its effective body mass and thus elevate its energy expenditures related to station-keeping. At the same time, drops hitting the wing area complicate wing movement, and their uneven distribution may negatively affect maneuverability. The acting forces of falling raindrops are directly proportional to their size and second power of their velocity; thus, the negative effect of rain rapidly increases with its intensity (Angulo-Martínez et al. 2016). Additionally, the negative consequences of striking droplets and plumage wetting are disproportionally higher for smaller flying animals. If we consider the high metabolic rate typical for small animals and the extreme costs of hovering flight (Lasiewski 1963, Evans and Thomas 1992), the energetic costs associated with hovering in the rain should be enormous.

To the best of our knowledge, there are only two studies describing how nectarivorous birds (hummingbirds) deal with intense rain. Ortega-Jimenez and Dudley (2012a) noted that Anna's hummingbird *Calypte anna* performs aerial and perched shaking to remove accumulated water from its body. Additionally, their research on the hovering performance of *C. anna* under increasing precipitation intensity demonstrates the hummingbird's capability to hover even under heavy rain (22.4 mm h^{-1}; Ortega-Jimenez and Dudley 2012b).

In this study, we focused on sunbird foraging behavior on *Impatiens sakeriana*. This plant is one of the enigmatic plants considered by Westerkamp (1990) to be adapted to hovering

birds in the Old World. Janeček et al. (2011) demonstrated that *I. sakeriana* is pollinated by two hovering sunbirds, and showed in a population of the Cameroon sunbird *Cyanomitra oritis* in the Bamenda highlands (Cameroon) that a bird's tendency to hover increases with increasing peduncle and pedicel length of the visited flower.

The aim of the present study is to expand our knowledge about the relatively well-framed (one plant–two pollinators) pollination system of *I. sakeriana* and evaluate some of the possible factors influencing hovering/perching decisions (herein referred to as foraging behavior) of both regularly visiting sunbird species, the Cameroon sunbird *Cyanomitra oritis* and the northern double-collared sunbird *Cinnyris reichenowi*. We tested whether: 1) the hovering/perching decision affects the flower visitation rate and therefore may influence energy intake, where we expected a positive relationship between energetic intake in time and hovering frequency to at least partly compensate for the higher energetic cost; 2) the hovering/perching decision is influenced by the architecture of the visited inflorescence, where we expected that long pedicels and peduncles (as plant traits that may enhance pollination effectiveness) would elevate the probability of being visited by a hovering sunbird; and 3) the hovering/perching decision is affected by actual precipitation, where we expected increasing rain intensity to lower the tendency of sunbirds to hover because of the extreme costs of flying in rain.

Methods

Study site

The study took place in Mount Cameroon National Park, southwest Region, Cameroon, at an elevation of 2100 m a.s.l. (4°8′N, 9°7′E), close to Mann's Spring. Mt Cameroon is a 4040 m a.s.l. high active volcano and one of the few remaining mountains with a primary forest cover from approximately 400 m a.s.l. (lowland rainforest) to approximately 2100 m a.s.l. (montane rainforest). Mt Cameroon is one of the rainiest places in the world. The highest mean annual rainfall is approximately 11 000 mm at the southwestern foot of the mountain and approximately 3000 mm in our study site near Mann's Spring (Maley and Brenac 1998). The vast majority of annual precipitation is concentrated within a single wet season, from April/May to October (Tye 1991, Maicher et al. 2020).

Target species

Impatiens sakeriana Hook. f. (Balsaminaceae) is a perennial herb reaching up to 3–4 m in height, though it is usually much lower. It is native to tropical western Africa and endemic to the mountains of western Cameroon and Bioko, where it grows in the moist shady places in mountain forests, at their edges and in shrubby vegetation along streams at altitudes ranging from 900 to 3000 m a.s.l. (Grey-Wilson 1980). Flowers, which are present throughout the year, are characteristically red with long spurs (up to 2.5 cm), and they are organized at the end of the long peduncle on much shorter pedicels in a subumbellate raceme. Flowers bloom gradually, and at one time, there are usually 1–2 open flowers per inflorescence. They generally produce a large volume (38 µl per 24 hours) of sucrose-dominant and relatively dilute nectar with a concentration of approximately 30% (Bartoš et al. 2012).

Cyanomitra oritis is a medium-sized sunbird, 9.8–13.8 g (10–14 g for the population on Mt Cameroon, unpubl.) and endemic to the mountain forests (1200–2100 m a.s.l) of eastern Nigeria, Cameroon and Bioko, where the species inhabits dense vegetation in forest clearings and shrubby patches (Cheke et al. 2001, Reif et al. 2007). The sexes of this species are similar, olive green with metallic steel-blue and yellow pectoral tufts on the head, throat and upper breast. They have a long (2.5–2.9 cm) and moderately downcurved bill and often feed on several *Impatiens* species (Janeček et al. 2015). This species has been recognized as the most effective pollinator of *I. sakeriana* in the Bamenda Highlands (Janeček et al. 2011).

Cinnyris reichenowi is a medium-sized, 5.2–8.0 g (7–10 g for the population on Mt Cameroon, unpubl.) sunbird and is common in mountain forests, their edges, clearings and gardens of west-central and northeastern Africa at elevations from 1200 to 2800 m a.s.l. (Cheke et al. 2001). Males of this species are brightly colored, with metallic green on the head, mantle and back and a red breast with a narrow blue or purple band below the throat; in contrast, females are inconspicuous and olive green in color with slightly paler underparts. Both sexes have relatively short bills (approximately 1.6–2.2 cm) and are known to feed on nectar from a variety of plants (Janeček et al. 2012, 2015, Nsor et al. 2019) as well as on insects and spiders. This species belongs among the most abundant in areas of higher elevations in western Cameroon (Reif et al. 2006, Sedláček et al. 2015).

Data collection

The data used were collected during August 2017 and August 2019. In the target area around Mann's Spring, we found 10 and 7 flowering individuals of *I. sakeriana* in 2017 and 2019, respectively. We recorded all their visitors for four days using VIVOTEK IB8367-T security cameras during 12-h periods (6:00–18:00; unless the recording failed). Altogether, we monitored 147 flowers.

The total number of open flowers differed between plants and changed during the day. Nevertheless, with only two exceptions, each monitored plant had more than one open flower each day. Using a measuring tape, we measured the linear distances between each pair of opened flowers (i.e. apertures of their corollas) and using a Vernier caliper, we measured the lengths of straightened peduncles and pedicels (further referred to as PedPed length), both with an accuracy of 1 mm.

The actual precipitation was measured in mm by two rain gauges placed in two different forest clearings within the area of selected plants; a photo of the water level in each was taken

every 10 min. During the 39.2 rainy hours (47.3% of the total measured time), the intensity of precipitation varied between 0.3 mm h^{-1} and 63 mm h^{-1}.

Recording was preceded by six days of mist netting in the closest neighborhood of chosen plants. Captured sunbirds were marked with metal rings and a unique combination of colored rings, and this information was used to approximate the number of individuals of each species arriving at the plants. The total number of individuals N_{total}, valid if all recorded individuals were to come repeatedly to feed on the monitored flowers, was calculated as $N_{total} = (N_{ringed} \times n_{total})/n_{ringed}$, where N_{ringed} is the number of ringed individuals recorded on the monitored plants, n_{total} is the total number of feeding events recorded and n_{ringed} is the number of feeding events of ringed individuals.

Energy intake estimation

We measured nectar consumption on eight different plants during 20 observation events distributed at different times over four days. During each event, one of us was hidden behind the vegetation several meters from the observed plant. When a bird arrived, we allowed it to visit 1–4 flowers (approximately half of the opened flowers) before chasing it from the plant. Total nectar volume was then measured in visited flowers and in the same number of unvisited flowers. Nectar was collected using 5 µl microcapillary tubes. If the nectar volume was sufficient, its sugar concentration was measured by a pocket refractometer (PAL-1, Atago Co.). The sugar amount per volume of nectar was calculated according to Galetto and Bernardello (2005). The average sugar consumption was estimated as the mean difference in sugar amount between non-visited and visited flowers. In those flowers, where nectar volume was not sufficiently high for measuring sugar concentration, an average concentration was used to estimate sugar amount. Energy gain per flower was calculated from the average sugar consumption per flower assuming the flowers to be sucrose dominant (Bartoš et al. 2012) and the nutritional value of sucrose to be 16.2 kJ g^{-1}.

Video processing

To detect visitor arrivals, we used the open source software MotionMeerkat (Weinstein 2015). Non-bird visitors and birds that obviously did not drink from at least one flower were ignored. We determined the species and color rings, if possible. We noted the type of behavior (hovering, perching or a combination of both) on the flower (from the insertion of the bill into a floral corolla to its extrusion) and while moving among flowers (from the extrusion of the bill from one floral corolla to its insertion to another floral corolla) and the exact time (in frames, i.e. 1/24 s) spent on each activity.

In total, we analyzed 720 h of video footage, i.e. 42.4 h per plant on average, even though there were slight differences in the time recorded on various days and plants. Due to some technical problems associated with the harsh environmental conditions, some of the recordings failed, resulting in four plants being recorded for fewer days.

Statistical analysis

To test whether the frequencies of the observed types of behavior of each sunbird species on a flower differ significantly from each other, we used the Chi-square test.

In all further analyses, only two types of behavior (hovering and perching) were included because the third type (a combination of both) did not occur frequently enough for comparison.

To investigate the effect of sunbird behavior on flower visitation rate, we used nested analysis of covariance (nested ANCOVA) with plant identifier as an error variable and sum of distance between visited flowers as a covariate. The visitation rate was logarithmically (ln) transformed to normalize its distribution. Because of the many zero values and impossibility of improving the data distribution, we tested the effects of bird species and their behavior on the nectar amount left after the bird visit using nonparametric mixed effect PERMANOVA with the plant identifier as a random factor. PERMANOVA was performed in the PERMANOVA program, which is an extension of the software PRIMER (Anderson et al. 2008). To determine the effect of behavior and sunbird species on the time spent per flower and on energy intake in time we used a generalized linear mixed model (GLMM) with plant ID nested in year as a random factor.

For analysis of the effects of sunbird species, PedPed length and precipitation on the type of sunbird behavior, we used a binomial GLMM (package lme4; Bates et al. 2015) with an assumed Bernoulli distribution, setting flower identifiers nested within an individual plant nested within a year as random factors. Average precipitation was logarithmically (ln + 1) transformed to reduce the skewness towards larger values, as we obtained many hours of recordings and visit events during light rain but only a few visit events in heavy rain.

Except for one, all statistical analyses were performed in R (<www.r-project.org>).

Results

Overall, we reported 1224 flower visits by *C. oritis* and 1392 flower visits by *C. reichenowi*. We noticed two ringed individuals of *C. oritis* on two different monitored plants, whose arrivals represented 12.1% of all arrivals of this species to any plant, and five ringed individuals of *C. reichenowi* on six of the monitored plants, whose arrivals corresponded to 54.2% of all arrivals of this species to any plant. Therefore, we assumed that we monitored a total of approximately 17 individuals of *C. oritis* and 11 individuals of *C. reichenowi*. However, we expect the real numbers to be slightly higher as only a relatively small fraction of the ringed birds appeared in the video recordings.

Table 1. Approximate energy gain over time and the effects of sunbird behavior (Be) and sunbird species (Sp). Differing letters above the means ± SDs indicate significant differences between groups (t-tests with Bonferroni p-value adjustment). * $0.01 < p < 0.05$; ** $0.001 < p < 0.01$; *** $p < 0.001$. We assumed an average sugar consumption of 0.36 mg and an average energy gain of 5.83 J per flower (see text for explanation).

	Cyanomitra oritis		*Cinnyris reichenowi*		GLMM		
	Hovering	Perching	Hovering	Perching	Be	Sp	Be × Sp
Time spent on a flower [s]	a 0.67 ± 0.31 n=653	b 0.79 ± 0.43 n=356	c 0.92 ± 0.48 n=862	d 1.43 ± 0.81 n=442	***	***	**
Time spent moving between two flowers [s]	a 1.38 ± 1.9 n=253	a 1.48 ± 0.97 n=113	b 2.08 ± 1.98 n=343	c 3.24 ± 2.17 n=144	ns	***	ns
Total time per flower [s]	a 2.04 ± 2.01 n=253	a 2.17 ± 1.06 n=113	b 2.98± 2.09 n=343	c 4.82 ± 2.44 n=144	***	**	*
Estimated energy gain in time [J s^{-1}]	a 4.69 ± 3.11 n=253	b 3.32 ± 1.56 n=113	b 2.78 ± 1.65 n=343	c 1.59 ± 0.90 n=144	***	ns	***

For both species, the most frequent behavior performed while feeding on a flower was hovering (*C. oritis*: $\chi^2 = 57.51$, df = 2, $p < 0.001$; *C. reichenowi*: $\chi^2 = 44.01$, df = 2, $p < 0.001$). *Cyanomitra oritis* hovered during 62.8% of all flower visits, and *C. reichenowi* during 57% of all flower visits. Perching on any available perch was performed during 36.1% of visits by *C. oritis* and 39.3% of visits by *C. reichenowi*. Both species rarely (in 1.1% and 3.8% for *C. oritis* and *C. reichenowi*, respectively) performed the combination of hovering and perching during one flower visit.

The frequency of hovering differed significantly between species ($\chi^2 = 58.48$, df = 1, $p < 0.001$; Table 2). In general, a higher hovering frequency was correlated with a higher flower visitation rate ($F = 89.37$, df = 1, $p < 0.001$; Fig. 1). If counted per minute, the mean number of visited flowers would differ by 7.9 for *C. oritis* ($F = 11.98$, df = 1, $p < 0.001$) and by 11.4 for *C. reichenowi* ($F = 96.21$, df = 1, $p < 0.001$). We also found the effect of the interaction between species and hovering frequency on the flower visitation rate to be significant ($F = 13.47$, df = 1, $p < 0.001$). The mean flower visitation rate was lower for *C. reichenowi* ($F = 16.21$, df = 1, $p < 0.001$), as the speed of flower visitation by an individual of this species was, on average, only 21.1 flowers per minute, while an individual of *C. oritis* visited, on average, 33.6 flowers during this time.

The average nectar residual after the bird visit did not differ according to the species of bird visit or the type of behavior on the flower (mixed-effect PERMANOVA, bird species: pseudo-F = 1.80, p = 0.12; behavior: pseudo-F = 0.02, p = 0.90, interaction: pseudo-F = 0.02, p = 0.90). Therefore, the average sugar (0.36 ± 0.47 mg) and energy (5.83 J) intake per flower was considered to be the same for both species and all types of behavior. Consequently, the estimated energy intake in time differed (according to the total time spent per flower; Table 1) significantly between the two types of behavior ($F = 183.34$, df = 1, $p < 0.001$). The interaction between behavior and species was also significant ($F = 21.34$, df = 1, $p < 0.001$).

Table 2. Effects of bird species and peduncle plus pedicel length (PedPed) on sunbird behavior. Three types of models differing in types of perches considered. Significant results ($p<0.05$) are shown in bold.

	Stem of the visited flower		All stems of the visited plant		All stems of the plant or peduncle	
	χ^2	p	χ^2	p	χ^2	p
Bird species (BS)	42.65	**< 0.001**	41.74	**< 0.001**	58.48	**< 0.001**
PedPed (PP)	0.81	0.67	2.49	0.29	3.34	0.19
BS × PP	0.74	0.39	0.88	0.35	0.32	0.57

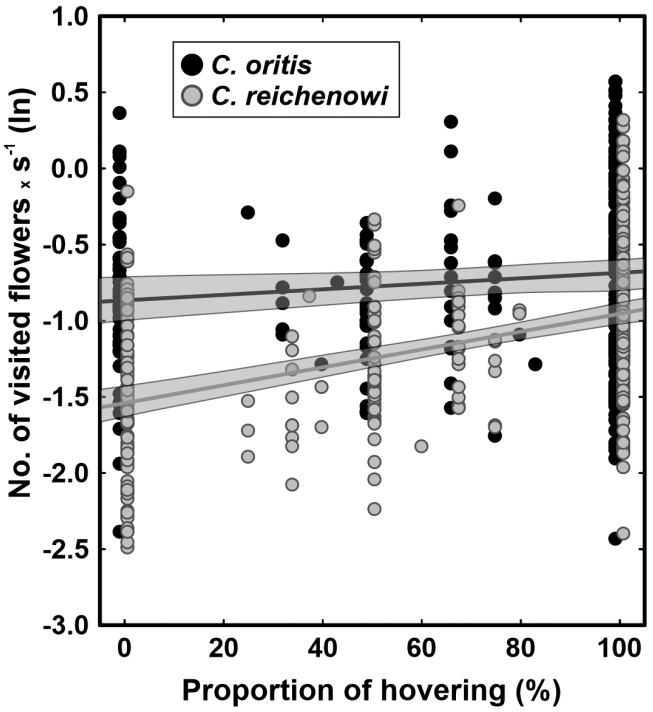


Figure 1. The relationship between the number of visited flowers per second (logarithmically transformed) and the proportion of hovering during one plant visit. Gray areas indicate the 95% confidence intervals.

On average, *C. oritis* visited flowers with a PedPed length of 13.09 ± 4.10 cm, and *C. reichenowi* visited flowers with a PedPed length of 11.51 ± 2.48 cm (t-test; t = 9.74; df = 1379.6; p < 0.001). The longer PedPed length of a flower significantly increased the probability of hovering only when visited by *C. reichenowi* and if all parts of visited *Impatiens* were included in the analysis as possible perches ($\chi^2 = 5.23$, df = 1, p = 0.02). Figure 2 shows an almost identical observed pattern for *C. oritis*; however, this difference was not significant ($\chi^2 = 2.326$, df = 1, p = 0.51). We did not find any significant relationship when including only the stem of visited flowers or all stems of visited plant individuals in the analyses (Table 3).

A total of 30.7% of all floral visits by *C. oritis* and 36% of all floral visits by *C. reichenowi* occurred under light rain (0.1–2.5 mm h^{-1}), 7.3% of all floral visits by *C. oritis* and 20.2% of all floral visits by *C. reichenowi* occurred under moderate rain (2.5–7.5 mm h^{-1}), and 7.3% of all floral visits by *C. oritis* and 7% of all floral visits by *C. reichenowi* occurred during heavy rain (7.6–50 mm h^{-1}). We did not find any effect of the interaction between sunbird species and precipitation on bird behavior on a flower ($\chi^2 = 0.02$, df = 1, p = 0.88). However, increasing precipitation slightly lowered the hovering frequency of *C. reichenowi* ($\chi^2 = 4.97$, df = 1, p = 0.03), while no such trend was found for *C. oritis* ($\chi^2 = 0.13$, df = 1, p = 0.72; Fig. 3).

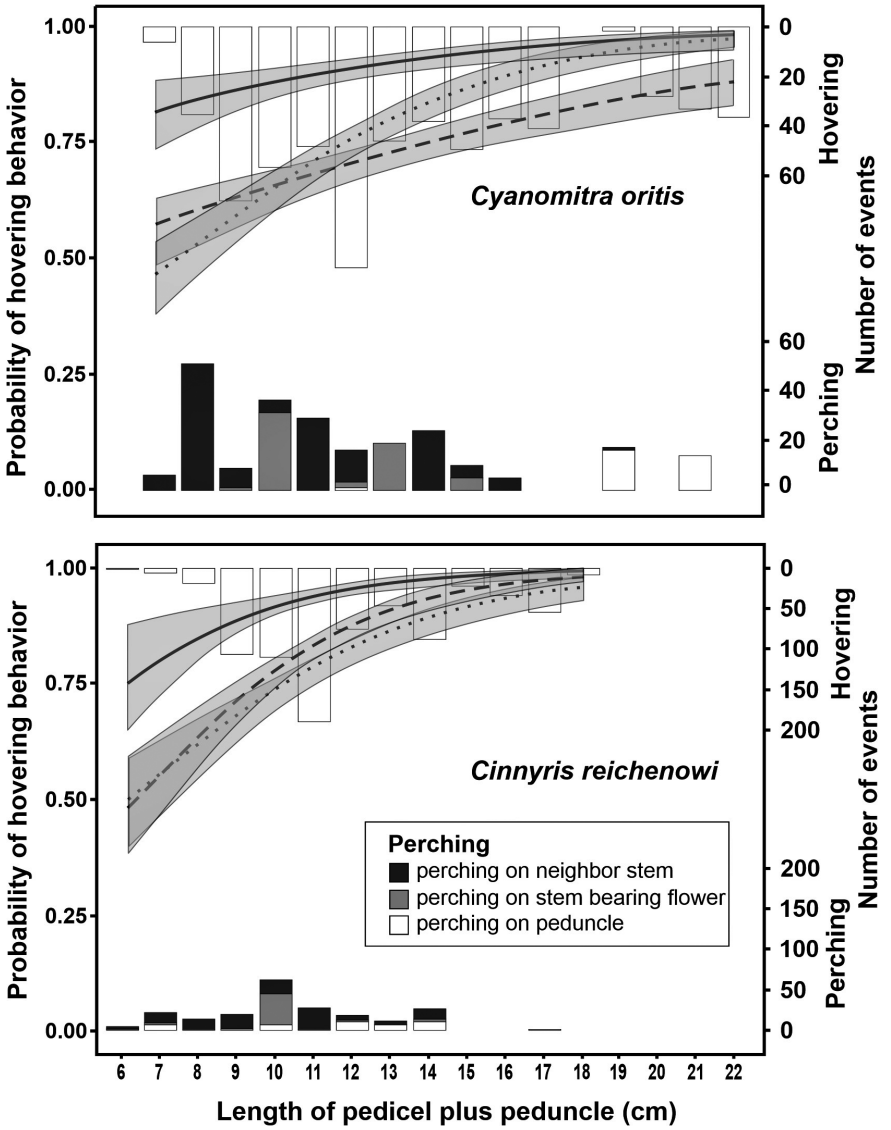


Figure 2. The probability of hovering on a flower as an effect of peduncle plus pedicel (PedPed) length. Different types of perches are represented by different colors, and bars represent the total number of observed cases of hovering (up) and perching (down). The full line represents the regression if only perching on the stem of the visited plant is considered, the dotted line represents the regression if perching on any stem of the visited plant is considered, and the dashed line represents the regression if perching on any stem or peduncle of the visited plant is considered. Gray areas indicate the 95% confidence intervals.

Table 3. Effect of peduncle plus pedicel (PedPed) length on the foraging behavior of *C. oritis* and *C. reichenowi*. Three types of models differing in types of perches considered. Significant results (p<0.05) are shown in bold.

	Stem of the visited flower		All stems of the visited plant		All stems of the plant or peduncle	
	χ^2	p	χ^2	p	χ^2	p
C. oritis						
PedPed	0.061	0.805	0.75	0.387	0.43	0.512
C. reichenowi						
PedPed	0.207	0.65	1.34	0.247	5.231	**0.022**

Discussion

Both sunbird species hovered in the majority of flower visits (*C. oritis* in more than 60% and *C. reichenowi* in slightly less than 60% of visits). These numbers are higher than the observations in the Bamenda Highlands, where *C. oritis* hovered in slightly more than 50% of flower visits and *C. reichenowi* in approximately only 35% of all flower visits (Janeček et al. 2011, Padyšáková and Janeček 2016); these values are also higher than those previously recorded from Mt Cameroon, where *C. oritis* hovered during 35% of flower visits and *C. reichenowi* in 25% of flower visits (Janeček et al. 2015). Similar to the results of other studies, we also recorded *C. oritis* hovering more often than *C. reichenowi*.

Energetics

For both sunbird species, we found hovering to be accompanied by a higher flower visitation rate, as has already been demonstrated for hummingbirds and honeyeaters (Pyke 1981). A higher proportion of hovering on a plant was associated with both shorter time spent on flowers and shorter time spent moving between flowers (Table 1). This finding supports the idea of Padyšáková and Janeček (2016), who stated that frequent hovering could accelerate pollination. The higher speed of flower visitation of *C. oritis* compared to *C. reichenowi* may be associated with body size and is in accordance with studies showing that *C. oritis* is a more effective pollinator of *I. sakeriana* (Janeček et al. 2011) and never visits its flowers illegitimately (Janeček et al. 2015). The decrease in the speed of flower visitation with an increasing proportion of perching while feeding on flowers was species-specific, being more prominent for *C. reichenowi*.

The amount of consumed nectar did not differ among flowers visited by hovering or perching birds. As hovering behavior ensured shorter handling times for the studied species, hovering while feeding is associated with a higher energetic intake per unit of time, but again, this relationship is species-specific (Table 1). On the other hand, energetic costs associated with hovering are expected to be much higher than those of perching (Lasiewski 1963, Prinzinger et al. 1989, Evans and Thomas 1992).

Pyke (1981) similarly estimated energetic intake in relation to the bird behavior for Australian honeyeaters (*Phylidonyris novaehollandie* and *P. nigra*) foraging on *Lambertia formosa* and American hummingbirds (*Selasphorus platycercus* and *S. rufus*) foraging on *Ipomopsis aggregata*. On both plants, the estimated energy intake per flower was slightly less than 2.5 times (*I. aggregata*) or almost nine times (*L. formosa*) higher than the values obtained in our study. The author revealed that due to their higher body mass and plant characteristics, such as sugar content per flower and inter-flower or inter-inflorescence distances, the net energy gain (J s^{-1}) for foraging honeyeaters, in contrast to hummingbirds, was lower when perching (Pyke 1981). Therefore, the relatively low energy intake per flower of *I. sakeriana* (if compared to both *L. formosa* and *I. aggregata*) should favor perching by sunbirds. On the other hand, the relatively low body mass of *C. oritis* and *C. reichenowi* (compared to the abovementioned honeyeaters) and the position of flowers of *I. sakeriana* that are relatively distanced from each other (compared to *L. formosa*), according to his presumption, favor hovering in sunbirds. However, his theory does not explain the differences in hovering frequencies among sunbird species. Based on his presumptions, to maximize the net energy gain on the same plant, *C. reichenowi*, which has a lower body mass, should tend to hover more than the heavier *C. oritis*, which is exactly the opposite of what we observed. Taken together with the overlaps in distribution (Grey-Wilson 1980, Cheke et al. 2001) and the high pollination efficiency (Janeček et al. 2011), *C. oritis* and *I. sakeriana* could potentially share a longer evolutionary history, resulting in various adaptations on both sides. These adaptations may be connected with improved bird hovering ability, allowing faster pollination and new restrictive visitor filters for the plant.

According to a study by Riegert et al. (2011) focusing on the diurnal activity of sunbirds in the Bamenda Highlands (Cameroon) during the dry season, an average individual of *C. reichenowi* is active for an average 8.79 h per day, and approximately half of this time (49%) is spent nectar feeding. Our results indicate a difference in energy intake of 1.19 J s^{-1}, favoring hovering while feeding (Table 1). Thus, if a bird of this species hovered on all the visited flowers during the 4.3 h dedicated to feeding each day, it would consume 18.42 kJ more than if it solely perched. This amount of energy would cover the cost of 2.29 h of active flying (Padyšáková et al. 2017). Such a bird would spend 1.33 h feeding on flowers while hovering. If perching, it would spend almost the same amount of time, i.e. 1.28 h per day, on flowers, but it would visit considerably fewer flowers (3212 versus 5195) and spend more time on each of them. During this time (1.3 h), the difference in cost of flying would be by 6.67 kJ higher than the cost of perching/feeding (Padyšáková et al. 2017) and therefore could be fully covered by higher energy intake. Moreover, hovering could be an energy-saving strategy if there is no limitation by the number of opened flowers and the distance between them.

However, these calculations are only theoretical and disputable for several reasons. First, individuals of *C. reichenowi* do not feed exclusively on *I. sakeriana*, and

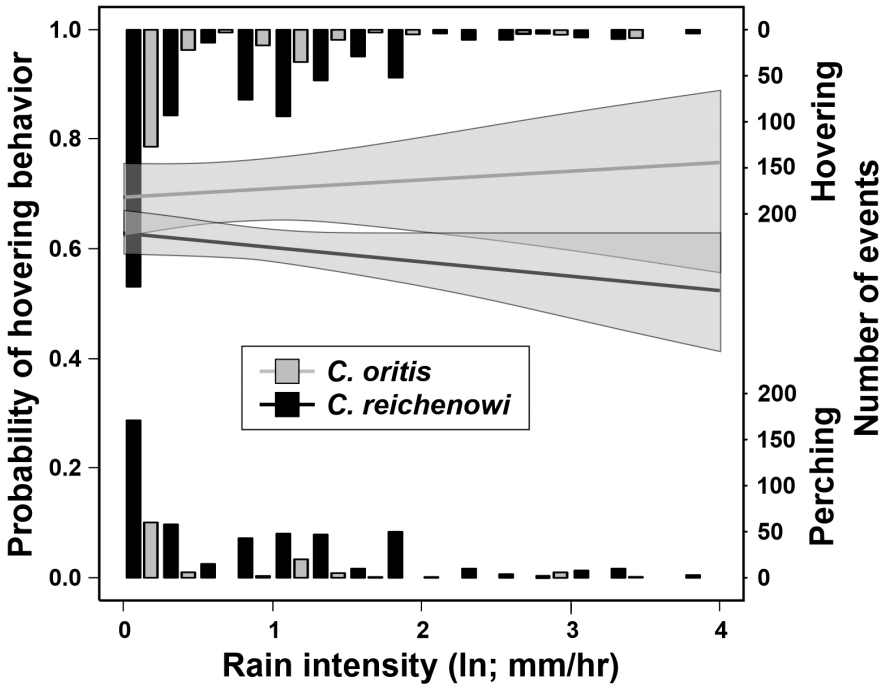


Figure 3. The probability of hovering on a flower in relation to the actual intensity of precipitation. Bars represent the total numbers of observed cases of hovering (up) and perching (down) on flowers. Gray areas indicate the 95% confidence intervals.

their preferences may vary seasonally. Their diurnal activity probably differs between seasons and between sexes as well. Sugar concentration in open flowers is lower in the rainy season (16.34% in our study versus nearly 30% in the dry season in Bamenda Highlands, Cameroon, according to Bartoš et al. 2012), which may affect handling time. Furthermore, we estimated the average energy costs based on body mass, but the metabolic rate during any mentioned activity was not measured. We included energy expenditure during active flying but did not take into account the actual speed of flying, which seems to be important as well (Evans and Thomas 1992). Therefore, all the estimates obtained here are approximate values. Similar estimates of *C. oritis* would be even more unprecise since, to the best of our knowledge, there are no data on the diurnal activity of this species. Before making any conclusions regarding the profitability of hovering during feeding, exact energetic costs associated with both strategies (i.e. hovering and perching) should be measured.

PedPed length

A trend of increasing probability of hovering with the lengths of peduncles and pedicels is apparent for both species. However, it is significant only for *C. reichenowi*, and only if all perching on all the stems of the visited plant, plus its peduncles, were considered. Thus, at least for this species, our results support the hypothesis of Miller (1985) and Westerkamp (1990) that visitor behavior is influenced by plant architecture.

The average PedPed length of flowers visited by *C. reichenowi* was markedly shorter than that of flowers visited by *C. oritis*. It seems that extremely long pedicels and peduncles alter the visitation frequencies of each sunbird species in favor of *C. oritis*.

In contrast to Padyšáková and Janeček (2016), we did not find any relationship between the PedPed length and behavior of *C. oritis* to be significant. We assume that the important factor behind these differences could be the study site. Our study took place on Mt Cameroon (southwest Region), while the study of Padyšáková and Janeček was situated in the Bamenda Highlands (northwest Region). Both mountains are isolated, and together with others, they create isolated islands of inland mountains with specific evolutionary processes, which can be reflected in the morphological and behavioral traits of individual populations. The PedPed values of *I. sakeriana* found on Mt Cameroon were significantly longer than those found in the Bamenda Highlands (t-test; $t = -5.92$, $df = 201.36$, $p < 0.001$), which was correlated with the higher hovering frequency we observed on Mt Cameroon (but see Janeček et al 2015). It has been noted previously that the *C. oritis* population inhabiting Mt Cameroon, which is considered a local subspecies (Cheke et al. 2001), has larger bills than those of *C. oritis* from other mountainous areas of Cameroon and Bioko (Smith et al. 2000).

Rain intensity

The percentage of floral visits under rain of any intensity (45.3% and 63.3% by *C. oritis* and *C. reichenowi*, respectively) more or less corresponds to the percentage of rainy hours out

of all hours when rain was measured (60% in 2017, when the most visits by *C. reichenowi* were recorded and 29% in 2019 when close to 2/3 of the visits made by *C. oritis* during the rain analysis were recorded) and thus supports the premise of Stiles (1978), who stated that vertebrates may play an important role as pollinators in wet conditions. Furthermore, both studied species were repeatedly recorded hovering under precipitation exceeding 20 mm h^{-1} (Fig. 3), which indicates their capability to hover under heavy rain in a way that is comparable to hummingbirds (Ortega-Jimenez and Dudley 2012b). Surprisingly, there were four hovering events on a flower by *C. reichenowi* even at precipitation intensities over 40 mm h^{-1} (compared to three perching events). However, the absolute values of the rain intensity should be considered with caution. Rain intensity was measured out of the canopy, and as a consequence, the intensity can differ locally depending on the vegetation cover above the hovering bird.

As expected, with increasing precipitation, birds of *C. reichenowi* tended to perch slightly more. We did not find any relationship between the intensity of precipitation and the behavior of *C. oritis*, which may imply this species is better adapted to intense rainy conditions. However, the smaller effect of rain on hovering frequency in this species could also be associated with its higher body mass since the acting forces of falling raindrops could have a relatively smaller effect on a bird's stability and thermal losses.

Conclusion

Our observations contradict the long-term standing paradigm that sunbirds rarely hover while feeding. We show that hovering on flowers can be associated with markedly shorter handling times, higher visitation speed and therefore higher energy intake in time, which may possibly compensate for the increased energetic costs of hovering compared to perching. However, the relationship is species-specific. According to our results, the dependence of perching/hovering decisions on plant architecture or actual precipitation is also species-specific. Both species can hover under heavy rain. However, to evaluate all the factors influencing sunbird foraging behavior and to obtain more precise estimates of the energetic costs associated with hovering and perching, more information on birds' diurnal activity, diet composition and energy expenditure during particular activities is needed.

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Data availability statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.cvdncjt4f> (Sejfová et al. 2021).

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