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PLANT-MICROBE-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Asymmetric competition for nectar between a large nectar thief and a small pollinator: an energetic point of view

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Abstract There are two alternative hypotheses related to body size and competition for restricted food sources. The first one supposes that larger animals are superior competitors because of their increased feeding abilities, whereas the second one assumes superiority of smaller animals because of their lower food requirements. We examined the relationship between two unrelated species of different size, drinking technique, energy requirements and roles in plant pollination system, to reveal the features of their competitive interaction and mechanisms enabling their co-existence while utilising the same nectar source. We observed diurnal feeding behaviour of the main pollinator, the carpenter bee *Xylocopa caffra* and a nectar thief, the northern double-collared sunbird *Cinnyris reichenowi* on 19 clumps of *Hypoestes aristata* (Acanthaceae) in Bamenda Highlands, Cameroon. For comparative purpose, we established a simplistic model of daily energy expenditure and daily energy intake by both visitor species assuming that they spend all available daytime feeding on *H. aristata*. We revealed the energetic gain–expenditure balance of the studied visitor species in relation to diurnal changes in nectar quality and quantity. In general, smaller energy requirements and related ability to utilise smaller resources made the main pollinator *X. caffra* competitively superior to the larger nectar thief *C. reichenowi*. Nevertheless, sunbirds are endowed with several mechanisms to reduce asymmetry in exploitative competition, such as the use of nectar resources in times of the day when rivals are inactive, aggressive attacks on carpenter bees while defending the nectar plants, and higher speed of nectar consumption.

Keywords Africa · Carpenter bee · *Cinnyris* · *Hypoestes* · Sunbird · *Xylocopa*

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Introduction

Nectar is an important resource of energy and nutrients for a large spectrum of flower visitors including bacteria, yeasts, mites, and diverse orders of insects, birds, reptiles and mammals. Nectar might, however, be temporally and spatially limited and in consequence interspecific competition will occur whenever the foraging of two or more organisms overlap in time and/or space (Brown et al. 1981; Galen and Geib 2007; Ramalho et al. 1991; Tiple et al. 2009). Such interactions are common in nature and play an important role in the organisation of guilds of nectar-feeding animals and the co-evolution of plant–pollinator relationships (Ferriere et al. 2007).

Competition for nectar raises the question of how sympatric nectarivorous organisms coexist, especially in situations when competition is expected to be highly asymmetric, for example when competitive interactions occur among distantly related taxa (Barnes 2003; Clutton-Brock et al. 1979; Paton 1993; Persson 1985). In general, a competitive advantage in exploitative competition is related to foraging economy, i.e., costs and benefits of foraging (Kodric-Brown and Brown 1979). From an energetic point of view, it is believed that animals of small body size and low energetic requirement might forage profitably even when the quantity of nectar per flower is insufficient for larger nectar feeders, and thus exclude larger competitors, especially if they are outnumbered (Heinrich 1975; Heinrich and Raven 1972). The typical example of such processes is disruption of native bird–plant interactions by invasive European honeybees in Australia (Paton 1993, 2000). There are, however, some ways for larger competitors to eliminate and even reverse this asymmetry. Firstly, larger animals may benefit from direct size effects and related ability to chase away smaller competitors. The two scenarios, when the smaller species are superior in exploitative competition or the bigger one in interference competition is supported by both theoretical models (Persson 1985) and field studies (Ford 1979). Aggressive behaviour during the defence makes sense only in situations when the saved nectar outweighs the cost in time and energy related to this behaviour (Wolf et al. 1975; Ford 1979, 1981; Kodric-Brown and Brown 1979). Based on this, it is not surprising that aggressive defending of nectar resources is mostly documented among closely related species of a similar size (Colwell 1973; Johnson and Hubbell 1974; Kodric-Brown and Brown 1978). In contrast, only a few studies have reported this behaviour among unrelated nectarivores (Jacobi and Antonini 2008; Ollerton and Nuttman 2013; Tropek et al. 2013). This kind of interference competition mostly happens between small birds and large insects (Boyden 1978; Lyon and Chadek 1971; Primack and Howe 1975; Tropek et al. 2013). Secondly, large visitors might have better adaptations that improve foraging economy, such as longer feeding apparatus enabling consumption of larger nectar amounts from tubular flowers, or better movement ability among flowers, decreasing handling time and increasing nectar intake speed (Inouye 1980; Temeles and Roberts 1993). Larger nectarivores usually have better thermoregulation which brings higher energetic requirements on one hand, but allows them to be active in conditions of low ambient temperatures and thus harvest nectar when smaller competitors are inactive. This advantage is particularly evident when large animals are foraging on plants which accumulate nectar during the night and/or increase production rates in the morning (Bartoš et al. 2012; Brown et al. 1981).

These competitive interactions are not only important from the visitors perspective, but also from the plants point of view. Individual nectarivore species play diverse roles in host plant reproductive systems. Only some visitors are effective pollinators (King et al. 2013; Padyšáková et al. 2013), whereas others either steal the nectar without pollen pick up or deposition, or illegitimately rob nectar by destruction of floral tissues (Brown et al. 2009; Irwin and Brody 1998, 1999, 2000; Navarro 2001; Traveset et al. 1998). This pattern leads to the question of what would happen if the ineffective visitor was competitively superior. In this case, the plant–pollinator system seems to be ecologically and evolutionary fragile and selection pressure on plant traits which will eliminate this superiority should occur (Jones et al. 2012). Irwin et al. (2008) highlighted that one of the important mechanisms can be the plant tolerance by increasing nectar production to decrease the competition and satisfy both pollinators and larcenists. In the systems where both larcenists and pollinators occur, detailed experimental and observational studies have shown that the effect of nectar robbing on pollinated hosts might be also positive (Irwin and Brody 1998). Considering this, it is rather advantageous for plants to maintain the equilibrium in competition between pollinators and larcenists. The dynamics of plant–pollinator–robber systems thus pose important selection pressures on the evolution of floral traits.

In this study, we assess competition for nectar between two unrelated visitors of the herb *Hypoestes aristata*. Our research to date indicates that although *H. aristata* is visited by many insect functional groups and also by sunbirds, especially *Cinnyris reichenowii*, this plant is in fact specialised to be pollinated by large bees (Janeček et al. 2012; Padyšáková et al. 2013). The carpenter bee *Xylocopa caffra* is both the most frequent and the most effective pollinator while the northern double-collared sunbird *C. reichenowi* does not affect the seed production of visited flowers (Padyšáková et al. 2013). Moreover, this sunbird species protects its favourable nectar sources by aggressively driving the carpenter bee out of *H. aristata* patches (Tropek et al. 2013).

Based on previous results, we tested the following predictions: (1) The smaller visitor and pollinator *X. caffra* will profit more from feeding on *H. aristata* because of lower energetic requirements and an ability to use smaller resources (i.e., plants with smaller number of flowers) (2) The sunbird will balance this asymmetrical competition by harvesting nectar in times when *X. caffra* is inactive, extracting higher amounts of nectar from individual flowers, and by higher speed of nectar intake (i.e., shorter handling time).

Methods

Study area

Our studies were conducted in the vicinity of Big Babanki, North-West Province, Cameroon (6°5′26″N 10°18′9″E) at high elevation in the central Bamenda Highlands (2100–2200 m a.s.l.). There is a single wet season from March to November, with annual precipitation ranging from 1 780 to 2 290 mm/year (For more details see: Cheek et al. 2000; Reif et al. 2007; Tropek and Konvicka 2010). The area is mostly comprised of open second growth of extensive pastures, frequently burned forest clearings dominated by *Pteridium aquilinum*, shrubby vegetation along streams, and remnants of species-rich tropical montane forests with a frequent occurrence of *Schefflera abyssinica*, *Schefflera manii*, *Bersama abyssinica*, *Syzygium staudtii*, *Carapa procera*, and *Ixora foliosa*.

Study species

The target plant species, *Hypoestes aristata* (Vahl) Sol. ex Roem. & Schult var. *aristata* (Acanthaceae), is a clonal herb that grows up to 1.5 m high and is native to tropical sub-Saharan Africa (Balkwill and Norris 1985; Hepper 1963). The flowers of *H. aristata* cumulate nectar in 1-cm-long, narrow corolla tubes. Nectar is hexose-dominant and the concentration is highly variable (30–45% w/w). The highest amounts of nectar can be found early in the morning but the highest nectar concentration is at midday (Bartoš et al. 2012). For more details about the plant see Padyšáková et al. (2013) and Bartoš et al. (2012). We studied *H. aristata* in the peak of its flowering season.

The northern double-collared sunbird *C. reichenowi* is distributed throughout West-Central and East Africa (Borrow and Demey 2001). This is the smallest of the local sunbirds and is the most abundant species in open woodlands, forest clearings and ecotones where a variety of flowering plants provide an energy supply in the form of nectar (Reif et al. 2006, 2007). Sunbirds are territorial but often exhibit off-territory forays for nectar (Riegert et al. 2014). Mismatch between small flowers of *H. aristata* and sunbird's bill and head morphology apparently causes ineffective pollination service (Padyšáková et al. 2013).

The medium-sized carpenter bee *X. caffra* is a widespread African species (Eardley 1983). This species, together with some other less frequent large bees, is the main pollinator of *H. aristata* (Padyšáková et al. 2013) as well as other plant species in the target area (Bartoš et al. 2015; Janeček et al. 2007). We have never observed carpenter bees gathering pollen while visiting the flowers of *H. aristata*.

The northern double-collared sunbird *C. reichenowi* is the most abundant bird species in our study area (Reif

et al. 2006). Riegert et al. (2014) estimated the breeding population in the area in November as between 30 and 35 breeding pairs/km^2. Similar estimation of carpenter bee's population size proved to be very difficult. We captured, marked and released tens of carpenter bees in the study area but the portion of recaptured marked individuals within the sample was extraordinarily low. We suppose that carpenter bees can fly long distances while foraging for nectar.

Field observations

Nineteen clumps at 6 different study sites, each within a 30-m radius were surveyed from November to December 2012 when the plants of *H. aristata* were in full bloom. The identical clumps were investigated in the same period in 2013. Clumps of equal quality but differing in total number of open flowers per clump were chosen to test the effect of resource size on visitation rates. Three clumps (four in one case) were observed simultaneously in 2-h sessions equally throughout 4 days (between 06h00 and 18h00) making 24 h per clump in total. Before each observation session, we counted the number of open flowers on studied clumps to know the availability of food supply. Since the number of flowers for individual clumps did not differ much during the study we used the mean number of flowers for a given clump as a measure of clump size (range 7–417 flowers per clump). While observing we focused only on visitations done by all individuals of the carpenter bee *X. caffra* and northern double-collared sunbirds *C. reichenowi*. During foraging bouts by visitors, we recorded the total time and the number of flowers visited per time unit. The total time measured included the time the species spent probing flowers and removing nectar as the major component, and the time among flowers within an inflorescence and some brief transits among inflorescences as a minor fraction.

Seven clumps of different numbers of flowers (within the same range of number of flowers per clump as observed clumps) were used to test the effect of clump size (number of flowers per clump) on nectar production and concentration. Several flowers were randomly bagged with fine mesh for 24 h to prevent nectar depletion by visitors. After this period, nectar volume accumulated in flowers, and nectar concentration, were measured and mean values per clump were used in analysis.

During the surveying period, we video-recorded target species feeding at *H. aristata* flowers. We aimed to record at least 10 specimens of each species and to collect at least 10 m of observation per individual to estimate the time proportion spent by sitting/feeding or by flight between individual flowering shoots. These proportions were used in calculations in our simplistic model of energy balance.

Table 1 Simplistic estimates of resting and flight metabolic rates for sunbird *Cinnyris reichenowi* and carpenter bee *Xylocopa cafra* based on equations shown

Species	Parameter	Estimated values	Equation used	References
Cinnyris reichenowi (8.6 g)	Resting MR			
	During the night	0.472 kJ/h	$nRMR = 0.102 \times M^{0.712}$	Prinzinger et al. (1989)
	During the day	1.46 kJ/h	$dRMR = M \times (277 - 4.3 \times T_a)$	Prinzinger et al. (1989)
	Sitting/feeding MR	2.92 kJ/h	Feeding MR $= 2 \times dRMR$	Paton (1980)
	Flight MR	8.05 kJ/h	$FMR = 1.14 \times M^{0.314}$	This study
Xylocopa caffra (0.768 g)	Resting MR	6.68 J/h	$RMR = 4.14 \times M^{0.66}$	Niven and Scharlemann (2005)
	Sitting/feeding MR	13.3 J/h	Feeding MR $= 2 \times RMR$	Paton (1980)
	Flight MR	845 J/h	$FMR = 20.1^a \times 129.94 \times M^{0.87}$	Niven and Scharlemann (2005)

[a] Caloric equivalent 20.1 J $\times$ mL^{-1} O$_2$ was assumed

Energy intake

To estimate the amount and concentration of nectar a carpenter bee or sunbird removed from a flower we chased it from a clump with more than 10 open flowers after it had probed minimally 3 flowers (mean 6 flowers). We then measured the nectar volume and concentration in the same number of visited and unvisited flowers using calibrated 5-µL microcapillaries and a pocket refractometer (ATAGO PAL-1; USA). Independently for each species, we calculated the difference ($V_R = A - B$) between (A) the nectar volume per unvisited flower in particular time of day and (B) the volume per visited flower in particular time of day. When the nectar volume was too low to measure the concentration we assigned the mean value appropriate for that particular time of day. To calculate the sugar concentration (in mg $\times$ µL^{-1} from w/w concentration (as established by the refractometer), we used an exponential regression equation (Galetto and Bernardello 2005). This allowed the specific energy value of nectar (E_{spec}) to be quantified in J $\times$ µL^{-1} (assuming that 1 mg glucose or fructose provides 15.6 J). Energy available in a flower (E_a) per visit by given species was calculated as

$$E_a = E_{spec} \times V_R \tag{1}$$

The obtained value was fitted by a 4th order polynom using a non-linear regression (STATISTICA 10) using the relevant time of the day as an explanatory variable (referred as E_h in the Eq. 2).

Simplistic model of energy balance

To compare competitive advantages of feeding on *H. aristata* between *X. caffra* and *C. reichenowii* we established a simplistic model of energy balance assuming that both species spend all available daytime feeding on this plant. The metabolic requirements of the carpenter bee and the sunbird were estimated using a published model that scales the requirements of other relevant species by a factor proportionate to body mass (see references in Table 1). The cover of daily energetic requirements of a given visitor species by nectar feeding was based on allometric scaling equation estimates of resting and flight metabolic rates (MR hereafter) and was calculated as follows:

$$\%Cover = \frac{\sum_{h=1}^{24} \frac{E_h}{\text{freq}}}{MR_{resting} \times t_{resting} + MR_{flight} \times t_{flight} + MR_{feeding} \times t_{feeding}}, \tag{2}$$

where %cover is the cover of daily energy requirements of an average individual sunbird or carpenter bee by nectar feeding, numerator is the modelled daily energy intake in (J) and denominator is modelled daily energy expenditure (J), E_h is modelled rate of energy available in a flower at particular time of the day (J), freq is flower visit frequency (h^{-1}), t_x is number of hours per day spent by activity 'x' and h is the hour of the day. The calculations and values of resting and flight MR used in this study are summarised in Table 1. For *C. reichenowi*, the flight MR data were derived from fitted non-linear regression of nectarivorous birds (Hambly et al. 2004). Regression was performed in STATISTICA 10. For *X. caffra*, we assumed night-time metabolism to be equal to resting MR. For both species in the daytime, flight MR was assumed while flying, and double resting MR while sitting/feeding (Paton 1980).

Statistical analyses

Count data (number of flowers per plant, number of visits per plant, number of visited flowers per plant, accumulated nectar volume per flower) were log transformed to improve normality. Most analyses were done in STATISTICA 10 (StatSoft 2013). The data on nectar remnants (nectar volume left after visitation) with many zeroes did not meet normality assumption even after transformation and in this

case we used the non-parametric permutation ANOVA in the programme PERMANOVA + for PRIMER (Anderson et al. 2008).

Results

In total, we recorded 365 visits of sunbirds *C. reichenowi* and 185 visits of carpenter bees *X. caffra*. In terms of flowers, *C. reichenowi* visited 14,192 and *X. caffra* 3517 flowers. Data gathered in individual years nevertheless did not significantly differ so we pooled them in subsequent analysis. We found no consistent sexual differences in nectar removal so we combined our data for both sexes of the sunbird species. 99% of carpenter bee visits were done by females. The amount of nectar left after one visit did not differ between sunbirds and carpenter bees (PERANOVA, Pseudo-$F_{(1,137)} = 0.4$; $p = 0.53$). Similarly, both species left on average 15% of the nectar offered. Compared to *X. caffra*, *C. reichenowi* visited significantly more flowers per plant (ANOVA, $F_{(1,545)} = 83.1$; $p < 0.01$, Fig. 1a) as well as more flowers per second (ANOVA, $F_{(1,545)} = 164.2$; $p < 0.01$, Fig. 1b). Both *C. reichenowi* and *X. caffra* highly preferred *H. aristata* plants with larger number of flowers, with a marginally significant higher tendency in the case of sunbirds (GLM, Number of flowers: $F_{(1,34)} = 33.6$; $p < 0.01$; Number of flowers*Species: $F_{(1,34)} = 3.2$; $p = 0.08$; Fig. 2). Clumps with fewer number of flowers did not significantly differ in nectar production ($r = 0.0389$; $p = 0.93$) and concentration ($r = 0.2996$; $p = 0.51$) per flower from clumps with larger number of flowers.

The first foraging carpenter bees were occasionally spotted no sooner than 07h00, probably due to low ambient temperature and high condensed moisture caused by big difference between day and night temperatures typical for tropical mountain environments (Online Resource 1); their feeding activity peaked around midday. Conversely, sunbirds started to regularly forage with dawn and fed more or less evenly during the day with slight decrease of activity over midday when the energetic intake per flower was the lowest (Fig. 3).

During daytime *C. reichenowi* and *X. caffra* are theoretically able to visit on average 3,883 and 2,339 flowers per hour, respectively. Sunbirds spent about 8% of their feeding time on *H. aristata* by flight between individual shoots flowers and they were sitting and feeding during the remaining time. Whereas carpenter bees spent 67% of their feeding time by flight and sat only for a moment while at flowers. Under these circumstances, their theoretical daily energy expenditure (24 h) is 45.6 kJ per sunbird and 6.4 kJ per carpenter bee, respectively. Our estimation predicts that whole day feeding on nectar of *H. aristata* (12 h for sunbird and 11 h for carpenter bee, respectively) would result
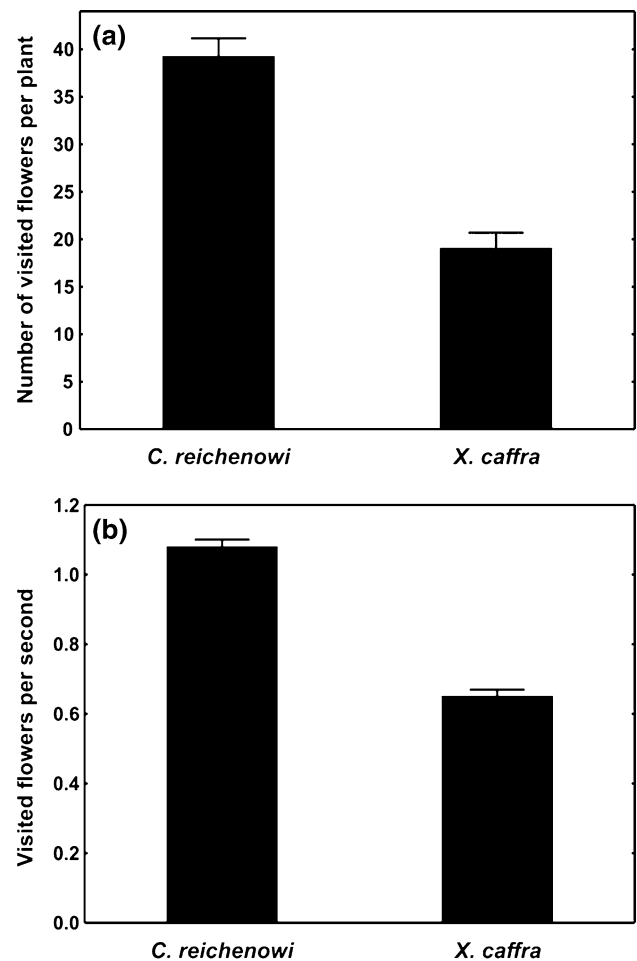
Fig. 1 The differences between *C. reichenowi* and *X. caffra* in numbers of visited flowers per plant (**a**) and visitation speed (**b**). *Error bars* represent standard error
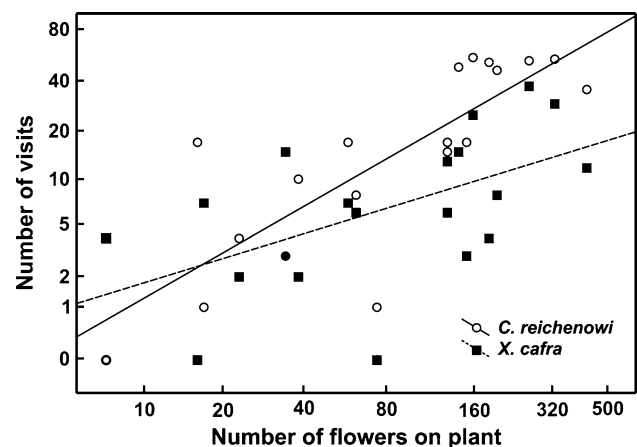
Fig. 2 Effect of number of flowers on plants of *H. aristata* on number of visits at these flowers. Both axes are log scaled
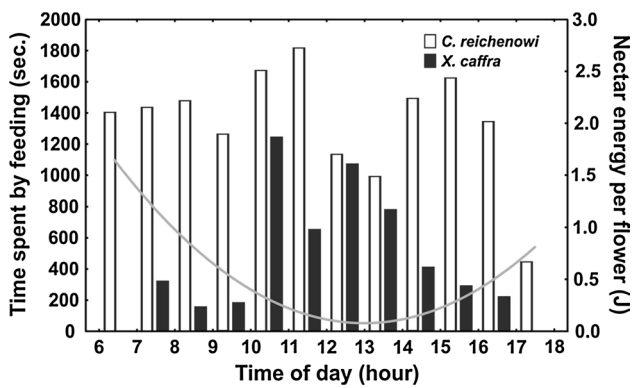
Fig. 3 Feeding activity of *C. reichenowi* and *X. caffra* (*bars*) and diurnal changes in standing crop (*grey line–polynomial function*)

in energy gain of 31.7 kJ for *C. reichenowi* and 8.5 kJ for *X. caffra*, respectively, and would thus cover 70% and 134% of their respective daily energy expenditure (see Figs. 4, 5 for more details).

Discussion

In our study, we reveal mechanisms underlying competition for nectar between the bigger nectar thief (sunbird) and the smaller pollinator (carpenter bee). Our simplistic model shows that this competition favours the smaller pollinator and as a consequence we support the hypothesis that smaller visitors are, thanks to lower energy requirements and related ability to exploit smaller resources, competitively superior in this case. In other words, the smaller species is able to meet its energy requirements more effectively and in shorter time, which makes the species favoured by exploitation competition (greater efficiency). Nevertheless, we also show many mechanisms that enable the larger competitor to reduce this superiority and avoid exclusion from the use of the resources. These mechanisms included interference competition (Tropek et al. 2013), use of resources in times when the smaller competitor is inactive, higher speed of nectar consumption, and higher preference for plants with larger number of flowers. Our results fully support Ford (1979) who observed competition interactions among nectar-feeding birds in Australia and suggested that the coexistence of the visitors is maintained by superiority of larger species in interference competition and of smaller species in exploitation competition.

Both empirical data and theoretical models show that body size has a predominant influence on an animal's energetic requirements, its potential for resource exploitation, and its susceptibility to natural enemies (Ballance et al. 1997; Bystrom and Garcia-Berthou 1999; Hamrin and Persson 1986; Werner 1994). Our study indicates that when
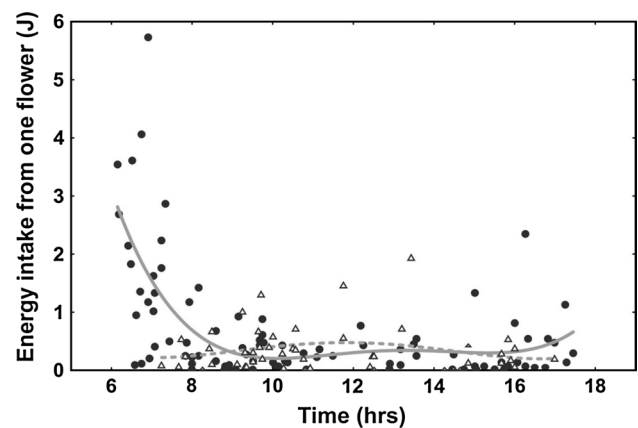
Fig. 4 Energy intake from one flower (J) by C. *reichenowi* (circles, full regression line) and *X. reichenowi* (*triangles*, *dashed* regression *line*) in the daytime fitted by quadratic polynomial function
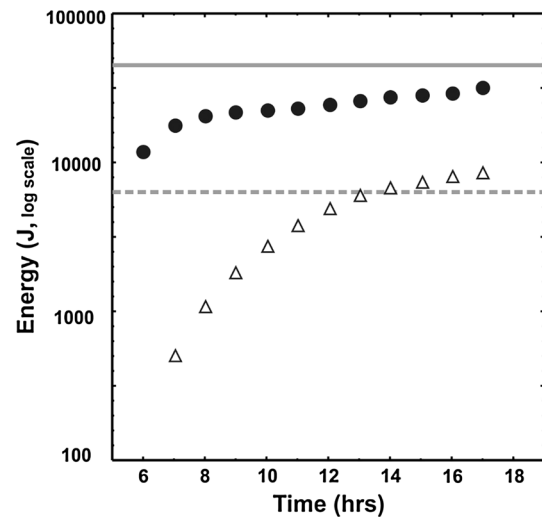
Fig. 5 Estimated daily energy expenditure (J) of *C. reichenowi* (*solid grey line*) and *X. caffra* (*dashed grey line*) together with cumulative energy intake by feeding at flowers in 1 h steps (*closed circles* for *C. reichenowi* and open triangles for *X. caffra*) assuming that the visitor will take nectar continuously during the day (06h00 to 18h00) from the flowers with nectar specific properties relevant at that time of day

competition is based on food depletion smaller species have greater net gain and are less affected by a decline in the food resource. This result is in agreement with experimental studies (Ballance et al. 1997; Persson 1985; Werner 1994) and in contrast to Schoener (1983). The smaller animal's advantage is best regarded as a combination of feeding ability as well as utilisation of limited resource availability (Persson 1985). In our case, when considering that a sunbird (weight 8.6 g) expends approximately 218 times as much energy as a carpenter bee (weight 0.768 g) just to cover its basal metabolism, and the mean energy load gained by each given species per one flower visit is

pretty similar (0.69 J for sunbird and 0.35 J for carpenter bee, respectively), our study clearly reveals the smaller harvester to be advantaged. Nevertheless, we should be aware that the results on energetic balances can change together with changes in many factors and it will be interesting to study these factors in the future. Nectar production and quality can be affected by factors like humidity, temperature or rain (e.g., Nicolson et al. 2007; Keasar et al. 2008), and increased abundance of visitors can decrease the plant profitability on individual level.

To counterbalance the exploitative losses, large dominant species often take advantage of a direct size effect and aggressively outcompete the smaller subordinate species in interference competition (Persson 1985). From this point of view interference competition is viewed as a consequence of asymmetrical exploitative competition (Persson 1985). The aggressive chasing of *X. caffra* by *C. reichenowii* in the studied system, firstly reported by Tropek et al. (2013) as well as observed occasionally during our study, together with competition asymmetry indicated by our simplistic model, supports this idea. This behaviour, nevertheless, in comparison with 185 observed visits of *X. caffra* can be seen as rather rare. Since intensive defending is a very costly strategy (Gill and Wolf 1975), an aggressor should optimally defend areas of highest productivity and tolerate smaller subordinate species to forage in less profitable areas (Ballance et al. 1997; Gill and Wolf 1975; Pimm et al. 1985; Riegert et al. 2011). In the study area, Riegert et al. (2014) described feeding niche partitioning between two local sunbird species, mostly driven by interference competition. The submissive sunbird *C. reichenowi* was forced by chasing from *Cinnyris bouvieri* to feed on plant species with relatively lower nectar productivity. Such a fundamental role of interference competition in organising of flower visitor communities was reported for honeyeater communities in Australia (Ford and Paton 1976, 1982; Ford 1979). Similarly, a previous study on sunbird–carpenter bee competition detected sunbirds' aggressive defending attacks to carpenter bees exclusively in high density patches (Tropek et al. 2013). Our current results complement the observed responses by showing sunbirds' stronger affinity to plants with more flowers (Fig. 2). As shown in many studies, differences in body size in terms of metabolic costs affect the higher preference of larger species to utilise and defend the richest food sources, maximising the foraging efficiency (Ballance et al. 1997; Gill and Wolf 1975; Palmer et al. 2003; Riegert et al. 2011; Tropek et al. 2013). This pattern might explain why chasing of insects by relatively large sunbirds (Ollerton and Nuttman 2013; Tropek et al. 2013) is reported much less often then chasing of insects by small hummingbirds (Jacobi and Antonini 2008; Primack and Howe 1975; Stoaks 2000).

Both species consumed and depleted food resource that was not later available for sympatric nectar-feeding rivals. One might argue that increased activity in the morning and again in the afternoon with cessation at midday by sunbirds reflects a normal pattern of bimodal daily bird activity (Bednekoff and Houston 1994) rather than consequence of exploitation competition. Field and laboratory studies, however, testing hummingbirds feeding throughout the day by recording their visits to artificial nectar feeders providing constant nectar source clearly showed that birds fed continually from early morning to late afternoon (Brown et al. 1981; Wolf and Hainsworth 1977). The diurnal pattern of sunbird feeding activity can be also affected by nectar chemical and physical properties. A recent study testing Baker's proposition (Baker 1975) on sunbird species strongly supported the hypothesis that the most efficient energy intake occurs at sugar concentrations that represent a compromise between low energy content and high viscosity (Koehler et al. 2010). The finding that nectarivorous birds should favour lower nectar concentration would correspond with observed values of *H. aristata* nectar in the morning and late afternoon (Bartoš et al. 2012). It seems to us that sunbirds midday cessation was a response to high nectar concentration and low volume, partly caused by carpenter bees' visits, which made them switch to other resources or to feeding on insects.

When considering low profit from exclusive feeding on *H. aristata* nectar (Fig. 4), sunbirds must visit other nectar plants producing higher caloric reward to cover its daily energy demands. Among them, *Hypericum lanceolatum* and *Lobelia columnaris* are typical components of the floral community within a sunbird territory and are two of the often visited plant species (Janeček et al. 2012) providing multiple larger nectar standing crop (Bartoš et al. 2012). This poses an interesting question: why does the sunbird clearly prefer (Janeček et al. 2012), actively defend (Tropek et al. 2013) and spend so much time of day feeding on a nectar source plant that does not meet its energy demands? Since some of the studied sunbird individuals were coloured ringed we could have occasionally observed that particular plants are visited regularly and by particular individuals and their mates. It implies that *H. aristata* nectar depletion is part of sunbird's territorial defence. Experiments with feeders found that birds responded to sudden sucrose solution loss (simulating competition) by increasing their visitation rate at that feeder (Garrison and Gass 1999; Gill 1988; Tiebout 1993). Similarly, Paton and Carpenter (1984) observed that rufous hummingbirds intensively deplete nectar resources in areas of the territory which are prone to intrusion. Moreover, Riegert et al. (2011), studying ordinary daily activities in northern double-collared sunbirds, observed a substantial percentage of time spent by active

insect feeding, reaching 15.4% in females. Studies on nectarivorous honeyeaters showed insects as a substantial part of the birds' diet especially in times when there is a shortage of nectar (Ford and Paton 1976; Armstrong and Perrott 2000). Using stable isotope analyses to detect diet and niche segregation among sympatric species in their study area, Procházka et al. (2010) revealed these sunbirds derive most of their nitrogen from invertebrates. We can hypothesize that this combination of sources provide sufficient energetic intake to cover the sunbirds overall metabolic expenditures as well as defending a less profitable resource, such as *H. aristata*, and is perhaps forced to do so by being excluded from other plants by larger sunbirds (Riegert et al. 2014). Our estimations show that the northern double-collared sunbird can be very susceptible to a decrease in flower density or nectar yield in *H. aristata*.

From the plant perspective, the optimal rate of nectar production should be the rate that yields the greatest difference between the costs and benefits of production (Zimmerman 1988). In our studied system, the plant species apparently produces much higher amounts of nectar per plant than would be necessary to satisfy energetic requirements of its mutualistic pollinator, the carpenter bee, and thus attracts thieving sunbirds as well. Excessive nectar production has most likely something to do with an established plant–pollinator–thief system as was suggested by other authors (Barrows 1976; Maloof and Inouye 2000; Morris 1996; Roubik et al. 1985). Although previous study has shown *C. reichenowi* as a directly ineffective pollinator, its presence in the visitor community might have some indirect effect on reproductive success of *H. aristata*. Recent studies have brought innovative evidence showing nectar robbers and thieves to not always have negative effects on seed set (Irwin and Brody 1999), but sometimes neutral or even positive outcomes via required increased pollen flow distances by changing the behaviour of the pollinators (Maloof 2001; Maloof and Inouye 2000; Richardson 2004). This view partly modifies the suggestion made elsewhere (Heinrich 1975) that natural selection would tend to produce enough food reward for the optimal pollinator, and at the same time, would not provide too great a food quantity to force a pollinator to make flower to flower and plant to plant movements. Natural selection for sufficiently low production of nectar expected in mutualistic relationships can be substituted, in case of plant–pollinator–thief system, rather by regulation of thieving members in the system. Although we do not have direct evidence we consider that this would also be the case in our system. We hypothesize that the accurate amount of food reward is maintained by sunbirds and in consequence carpenter bees move more often between plants to match their daily energy budgets. This hypothesis should, nevertheless, be tested in further experimental studies.

Author contribution statement EP, ŠJ, MB conceived and designed the experiments, and conducted fieldworks. ŠJ performed statistical analysis. JO developed the mathematical models. MB collaborated in making models and analysis. EP, ŠJ, JO wrote the manuscript; other authors provided editorial advice.

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