ORIGINAL ARTICLE

Food niche differentiation in two syntopic sunbird species: a case study from the Cameroon Mountains

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Abstract Closely related bird species can coexist in areas of range overlap due to differentiation of their ecological niches. If coexisting species have similar habitat requirements, separation of food niches presumably plays a crucial role. Theoretically, two possible food niche separation scenarios are possible: (1) use of different food resources or (2) temporal differences in feeding activity. We examined these mechanisms by investigating the feeding habits of two short-billed sunbirds (*Cinnyris reichenowi* and *C. bouvieri*) coexisting locally in the Bamenda Highlands, NW Cameroon. Daily feeding activity in both species showed a similar pattern, with two peaks (0800–0900 hours and 1500–1600 hours, respectively) and a prominent decrease in activity between 1100 and 1400 hours. However, the studied species clearly differed in their exploitation of plant resources. *C. bouvieri* mostly visited *Lobelia columnaris*, while *C. reichenowi* regularly visited three plant species, namely, *Hypericum revolutum*, *Hypoestes aristata* and *Impatiens sakerana*, with the most time spent at the second species. Such resource partitioning was probably caused by interspecific aggressive behaviour, since *C. bouvieri* actively repelled *C. reichenowi* from *Lobelia columnaris* plants, forcing *C. reichenowi* to feed on other plant species.

Zusammenfassung Nahe verwandte Vogelarten können in Gegenden, in denen sich ihre Vorkommen überschneiden, aufgrund einer Differenzierung ihrer ökologischen Nischen koexistieren. Falls koexistente Arten ähnliche Ansprüche an den Lebensraum aufweisen, kommt einer Trennung der Nahrungsnischen höchst wahrscheinlich die Schlüsselrolle zu. Theoretisch sind zwei mögliche Szenarien der Nahrungsnischentrennung denkbar: (1) die

Communicated by T. Friedl.

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Nutzung unterschiedlicher Nahrungsressourcen, oder (2) zeitliche Unterschiede in der Nahrungsaufnahme-Aktivität. Wir erforschten diese Mechanismen indem wir die Ernährungsgewohnheiten zweier kurzschnäbliger Nektarvogelarten (*Cinnyris reichenowi* and *C. bouvieri*), die im Bamenda Hochland, Nordwestkamerun lokal gemeinsam vorkommen, untersuchten. Die tägliche Nahrungsaufnahme-Aktivität folgte bei beiden Arten einem ähnlichen Muster mit zwei Gipfeln (zwischen 08:00–09:00 bzw. 15:00–16:00 Uhr) und einem deutlichen Aktivitätsabfall zwischen 11:00 und 14:00 Uhr. Die beiden untersuchten Arten unterschieden sich aber klar in der Ausnutzung der Pflanzenressourcen. *C. bouvieri* besuchte überwiegend *Lobelia columnaris*, wohingegen *C. reichenowi* drei Pflanzenarten regelmäßig besuchte: Hypericum revolutum, Hypoestes aristata und Impatiens sakerana, dabei verbrachte sie an der zweiten Art die meiste Zeit. Diese Art der Ressourcenaufteilung hatte ihre Ursache wahrscheinlich in interspezifischem Aggressionsverhalten, da *C. bouvieri* und *C. reichenowi* aktiv von Pflanzen der Art *Lobelia columnaris* vertrieb und *C. reichenowi* dadurch zwang an anderen Pflanzenarten zu fressen.

Introduction

Closely related bird species can coexist in areas of range overlap due to differentiation of their ecological niches (Tokeshi 1999). If syntopic animal species have similar habitat requirements, the separation of food niches presumably plays a crucial role in their coexistence (Schoener 1965; Moermond 1979; Huey and Pianka 1981; Alatalo et al. 1985; Alatalo and Moreno 1987). Nectarivorous species make suitable avian models to study food niche separation because they have well-defined and easily observable food resources. African sunbirds are small nectarivorous species living in various habitats, ranging from the forest interior to dry savannah. Their syntopic occurrence is a common feature throughout their ranges, and particular species demonstrate an affiliation to a specific variety of plants (Gill and Wolf 1977; Symes et al. 2008; Geerts and Pauw 2009a). In general, African sunbirds are less morphologically specialized for nectar feeding than New World hummingbirds (Cheke et al. 2001), as evidenced by their decreased morphological variation in bill or jaw size (Fleming and Muchhala 2008). In addition to feeding on nectar, they forage for invertebrates by leaf-gleaning or sallying like flycatchers (Cheke et al. 2001; Procházka et al. 2010). Theoretically, two possible food niche separation scenarios are possible: (1) use of different food resources or (2) temporal differences in feeding activity. In sunbirds, the first possibility is represented by

species' adaptations to different nectar resources, i.e., different plant species or a different proportion of nectar versus insect feeding. An example of this is the long-billed Malachite Sunbird (*Nectarinia famosa*, Linnaeus 1766), which has been found to prefer plants with longer nectar tubes (Geerts and Pauw 2009a), a result similar to the positive correlation found between hummingbirds' bill length and nectar holder length (Snow and Snow 1972). The second possibility is represented by differential exploitation of nectar resources over the course of the day (Symes et al. 2008) or during longer time periods, such as in the course of the breeding season or over years (Feinsinger 1976; Symes et al. 2008; Lara et al. 2009).

The most prominent mechanism responsible for feeding niche separation is interspecific competition. Nectarivorous birds show strong territorial behaviour, and they often compete for food resources (Gill and Wolf 1975; Feinsinger et al. 1985; Kay and Schemske 2003; Abrahamczyk and Kessler 2010). Hummingbird assemblages are modified by the degree of their specialization and availability of visited plants (Stiles 1975; Feinsinger 1978; Feinsinger et al. 1985; Arizmendi 1990) and by interspecific interactions. Feinsinger (1976) showed that one territorial hummingbird (Trochilidae) species modified all other species' patterns, thereby organizing the whole nectarivorous bird guild. Studies on Old World sunbirds are limited almost exclusively to South Africa (Nicolson and Fleming 2003; Brown et al. 2008; Symes and Nicolson 2008; Symes et al. 2008; Geerts and Pauw 2009b; Brown et al. 2010; Downs et al. 2010) and the Tanzania—Kenya region (Wolf 1975; Gill and Wolf 1977). These studies have mostly focused on physiological aspects of pollination behaviour (but see Young 1982; Burd 1994).

The aim of the study reported here was to test two alternative mechanisms of species coexistence by investigating the feeding behaviour of two syntopic short-billed sunbirds in the Cameroon Mountains. As aggressive behaviour may lead to niche partitioning of syntopic birds (Orians and Willson 1964), we focused on the extent of such behaviour. We therefore asked whether the species differ (1) in feeding habits (plant species use and nectar vs. insect feeding) or (2) in temporal patterns of resource exploitation (during the day and throughout the breeding season).

Materials and methods

Study site

The study site is situated in the Bamenda-Banso Highlands in the Mendongbuo area near Big Babanki village (Cameroon, NW Province, 6°5′N, 10°18′E, 2200 m a.s.l.). This

mountainous area was formerly covered in montane forest, but during the last 50 years the forest has almost completely disappeared due to logging (Ernest Vunan personal communication). The study area is approximately 0.5 ha, covered with stream mantel vegetation and surrounded by pastures and a *Pteridium aquilinum* community. The mean annual temperature is between 14.5 and 17.0°C, and mean annual precipitation varies from 1,780 to 2,290 mm. Most rain falls from March to November (Cheek et al. 2000).

Study species

Two sunbird species were studied: the Northern Double-collared Sunbird (*Cinnyris reichenowi*, Sharpe 1891) and the Orange-tufted Sunbird (*Cinnyris bouvieri*, Shelley 1877). The former inhabits mostly forest edges and scrub vegetation, while the latter often occupies more open terrain (Fry et al. 2000, Borrow and Demey 2001). In the study site, both species co-occur in a mosaic of open areas, forest fragments and stream mantel vegetation (Reif et al. 2006, Sedláček et al. 2007).

C. reichenowi occurs in the mountains of west-central and north-eastern Africa (Fry et al. 2000). The western subspecies *C. r. preussi* is heavier [*C. r. preussi*: males, 8.6 g; females, 7.5 g (this study); *C. r. reichenowi*: males, 6.8 g; females, 6.9 g (Cheke et al. 2001)] and has a longer bill than the eastern *C. r. reichenowi* [*C. r. preussi*: males, 19.4 mm; females, mean 19.0 mm; *C. r. reichenowi*: males, 16.2 mm; females, 15.0 mm (Cheke et al. 2001)]. *C. bouvieri* has a patchy distribution in Central Africa, and its geographical variability in bill length and body size is not known (Cheke et al. 2001).

In total, we caught and colour-ringed 24 individuals of *C. bouvieri* (2003: 13; 2007: 11) and 157 individuals of *C. reichenowi* (2003: 48; 2007: 109). The sunbirds were trapped using mist nets positioned nearby visited plants between 10 and 20 November of each study year. The study was carried out during pair formation, courtship, incubation and feeding of juveniles (personal observation).

The results of preliminary studies suggested that sunbirds mostly feed on the following plant species at our study site (Riegert et al. 2007): *Pycnostachys eminii* (Lamiaceae), *Lobelia columnaris* (Campanulaceae), *Hypoestes aristata* (Acanthaceae), *Hypericum revolutum* (Hypericaceae) and *Impatiens sakerana* (Balsaminaceae). *Hypericum revolutum* is the only species with flat, actinomorphic flowers; all of the other species have tubular zygomorphic flowers. *Impatiens sakerana* has spurred, zygomorphic flowers, which is typical for its family. According to Bartoš et al. (2009), the daily sugar content of nectar per flower for each plant species is, in order from highest to lowest (estimated daily nectar volume and sugar production per flower in parentheses): *Impatiens sakerana*, 13.92 ± 10.02 mg/µl (38 µl, 530 mg) > *Lobelia columnaris*, 11.25 ± 10.72 mg/µl (24 µl, 271 mg) > *Hypericum revolutum*, 6.73 ± 7.21 mg/µl (20 µl, 131 mg) > *Hypoestes aristata*, 0.99 ± 1.12 mg/µl (1 µl, 1 mg) > *Pycnostachys eminii*: 0.25 ± 0.22 mg/µl (<1 µl, <1 mg).

Sunbird observations

Observations of colour-ringed individuals of both sunbird species were carried out during the dry seasons of 2003 and 2007 from 19 November (2003) or 24 November (2007) until the end of the year (28 December). The observations were carried out at 36 non-overlapping observation points (20 points in 2003, 16 in 2007). Each observation point included individuals of all five focal plant species growing along a 10-m segment of stream mantel vegetation. We performed 30 observation sessions, each session consisting of 30 min of continual observation, at each observation point. During the course of the study period, the total observation time amounted to 200 h in 2003 and 160 h in 2007. Observation sessions were evenly distributed throughout the day as well as during the course of the study period. The observations were made at a distance of 10 m from the observed plants, and only sunbirds visiting plants within the observation points were recorded. In total, we gathered data on 2,749 observations of *C. bouvieri* and 11,865 observations of *C. reichenowi*. An activity was defined as one record of one type of behavioural activity of a sunbird individual with temporal information on its length. The following types of activities were distinguished during the observations:

1. *Nectar feeding*, when sunbirds visited plant flowers and used the nectar resources. The individuals repeatedly put their bills into flowers in the manner that enabled nectar exploitation.
2. *Insect feeding*, when the sunbirds visited plants or the bark of trees and they actively searched for insect food by gleaning while picking insects from the whole plant surface.
3. *Singing*, which was mostly exhibited by males, during defense of their territories.
4. *Self-grooming*, which included all activities bearing upon feather- and bill-cleaning.
5. *Aggressive behaviour*, which involved chasing intraspecific or interspecific rivals and mobbing attacks on nest predators.
6. *Perching*, which was observed usually after feeding and indicated resting of a sunbird individual.
7. *Other activities*, as represented by nest building, chick feeding and other behaviour related to reproduction.

Statistical analyses

Differences in bill length and body weight between the species were tested using analysis of covariance (ANCOVA; Statistica software ver. 2008, StatSoft, College Station, TX) using body weight and sex as the respective covariate. Aggressive behaviour was expressed as the numbers of interspecific and intraspecific events relative to the total number of all aggressive events. The results of interspecific aggressive events for plants (mainly *Lobelia columnaris*) were recorded. An individual was considered as the winner when the other was repelled from the plant. Intraspecific and interspecific aggressive events usually included chasing during flight. Other types of aggressive behaviour included mobbing and attacks on nest predators.

Multivariate analysis was used to address the first aim of the study, i.e. whether the sunbirds differ in use of plant species. The nectar feeding proportion for each sunbird individual at a plant species was calculated relative to the total time spent by that individual within a designated point. The data were analysed using redundancy analysis (RDA; Canoco software, ter Braak and Šmilauer 1998), with sunbird sex, calendar year and observer's individuality as covariates. The effect of sunbird species on flower use was tested using the Monte Carlo permutation test under 499 unrestricted permutations. Figure 1 shows the total proportion of nectar feeding at a plant species separately for each sunbird species. Overall data for behavioural activities were calculated as the percentages of total time spent by species (or sex) within designated points that allowed comparison of studied sunbirds (sexes) (Table 1). We used chi-square tests (Statistica software) for these comparisons.

The second aim, i.e. whether the sunbird species differ in nectar feeding activity during the day and over the course of the breeding season, respectively, was addressed by Wilcoxon matched pairs tests (Statistica software). As data units, we used the total proportion of nectar feeding (relative to the whole time spent by sunbird species within designated points) for all plants within a 1-h period (data unit for daily patterns, 0600–1800 hours) and the total proportion of nectar feeding and insect feeding for all plants in five day-periods. For the analyses, data from both years were pooled as no significant differences were found between their distributions (Wilcoxon matched pairs test, all $P > 0.6$).

Results

The species have similar body mass and bill length [mean ± standard deviation (SD); *C. reichenowi*: body weight, 8.1 ± 1.2 g; bill length, 16.0 ± 1.2 mm; $n = 157$; *C. bouvieri*: body weight, 8.3 ± 0.8 g; bill length, 17.3 ± 1.1 mm; $n = 24$]. Body weight did not significantly differ between the two species (ANCOVA, covariate sex, $P = 0.4$). Bill lengths did not differ significantly between sexes within a species (ANCOVA, covariate body weight, P at least 0.3), but they significantly differed between the species (ANCOVA, covariate body weight, $df = 1$, $F = 288.9$, $P < 0.0001$).

During observations, we recorded 1,396 intraspecific and 543 interspecific aggressive events. Intraspecific aggression was nearly always represented by the chasing of males at the border of a territory (85.4%) and female–female aggressive contact (14.6%). Most intraspecific aggressive events were recorded for the more abundant *C. reichenowi* (87.6%). Nearly half of the interspecific aggression events ($n = 245$) were recorded between the studied species (45.1%), while the rest of these aggressive events were directed against nest predators (mainly the Yellow-breasted Boubou *Laniarius atroflavus* Shelley 1887, Speckled Mousebird *Colius striatus* Gmelin 1789 and Green Bush Squirrel *Paraxerus poensis* Smith 1830). *C. bouvieri* individuals were usually the winners (88.6%) of aggressive events occurring at *Lobelia columnaris*.

Significant differences in plant use (e.g. proportion of time spent on nectar feeding) was observed between the two studied sunbirds (RDA $F = 52.35$, $P = 0.003$). *C. bouvieri* mostly visited *Lobelia columnaris*, whereas *C. reichenowi* regularly visited three plants (*Hypericum revolutum*, *Hypoestes aristata* and *Impatiens sakerana*), with the most time spent at the second species (Fig. 1). Females of both sunbird species showed a significantly higher proportion of nectar feeding than males (chi-square test: *C. bouvieri*, chi^2 = 7.519, $df = 1$, $P = 0.0061$; *C. reichenowi*: chi^2 = 16.164, $df = 1$, $P < 0.0001$), which was presumably due to the frequent singing activity of males (Table 1). Some interspecific differences in feeding behaviour were also observed. In total, *C. reichenowi* fed less on nectar than *C. bouvieri* (Chi square test: chi^2 = 4.8282, $df = 1$, $P = 0.0280$).
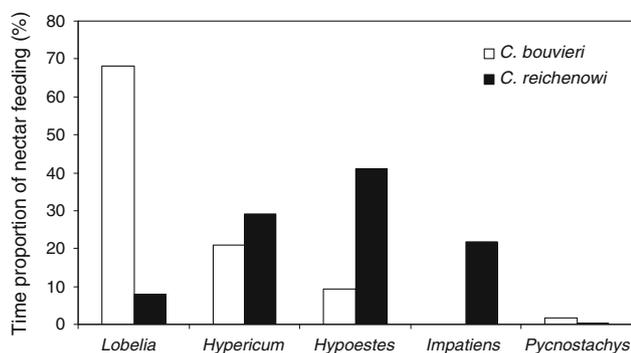

Fig. 1 Proportions of time spent nectar feeding at each plant by the two sunbird species (*Cinnyris reichenowi*, Sharpe 1891 and *C. bouvieri*, Shelley 1877). Data for observations made in 2003 and 2007 were pooled

Table 1 Proportion of time spent on different activities by two sunbird species in the Bamenda-Banso Highlands, NW Cameroon

Activity	Cinnyris bouvieri			Cinnyris reichenowi		
	Males	Females	Mean/sum	Males	Females	Mean/sum
Nectar feeding (%)	56.7	89.9	73.3	29.1	68.9	49.0
Insect feeding (%)	1.9	4.7	3.3	7.5	15.2	11.4
Singing (%)	31.7	0.3	16.0	41.0	2.8	21.9
Perching (%)	7.0	3.4	5.2	12.9	1.7	7.3
Self-cleaning (%)	0.5	1.6	1.1	1.3	1.5	1.4
Aggressive behaviour (%)	1.5	0.1	0.8	2.0	0.7	1.4
Other behaviour (%)	0.7	0.0	0.4	6.2	9.2	7.7
Number of visits (n)	2,215	534	2,749	7,914	3,951	11,865
Total activity time (min)	1,241	385	1,626	6,278	2,509	8,787

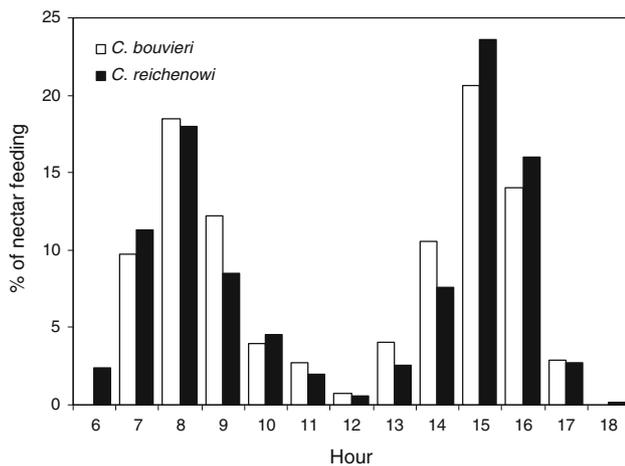Data for 2003 and 2007 were pooled

Fig. 2 Daily pattern of nectar feeding of studied sunbirds (% of time). Data for observations made in 2003 and 2007 were pooled

Analysis of nectar feeding activity over the day revealed a bimodal pattern in both species studied, with peaks at 0800–0900 hours and 1500–1600 hours and a prominent decline in activity between 1100 and 1400 hours (Fig. 2). The differences between species were not significant (Wilcoxon matched pairs test: $n = 13$, $Z = 0.035$, $P = 0.972$). A decreasing pattern of nectar feeding in both study species was found during the course of the observations (Fig. 3a). This pattern was similar for both studied sunbirds (not statistically different; Wilcoxon matched pairs test: $n = 8$, $Z = 1.260$, $P = 0.208$). In contrast, the proportion of activity devoted to insect feeding increased during the course of the observations (Fig. 3b). These between-species differences were also not significant (Wilcoxon matched pairs test: $n = 8$, $Z = 0.140$, $P = 0.889$).

Discussion

Both of the sunbird species observed in our study (*Cinnyris bouvieri* and *C. reichenowi*) showed great intra- and interspecific aggressivity. In general, intraspecific aggression
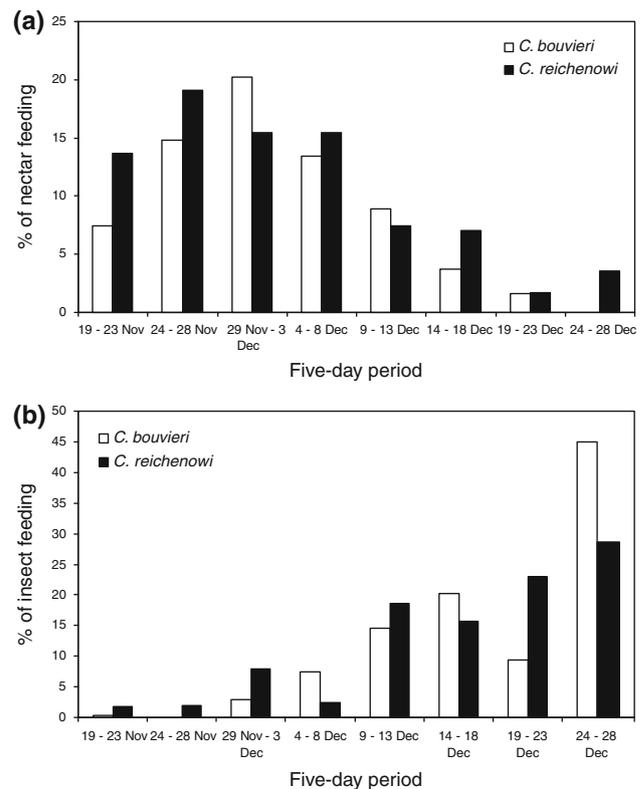

Fig. 3 Proportions of nectar feeding (**a**) and insect feeding (**b**) during each 5-day period (% of time). Data for observations made in 2003 and 2007 were pooled

was more common than interspecific events. This aggression may be due to the relatively higher density of *C. reichenowi* at the study locality compared with *C. bouvieri* (Reif et al. 2006; Sedláček et al. 2007). Interspecific aggression occurred less frequently, but probably played a key role in the coexistence of these sunbirds. Studies on New world hummingbirds (Feinsinger 1976; Hixon et al. 1983; Feinsinger et al. 1985) have found that such aggressive interactions are related to competition for nectar resources. This type of aggressive behaviour has also been observed in the Golden-winged Sunbird (*Nectarinia reichenowi* Fischer

1884) in Kenya. Individuals of this species were observed to actively defend their resources when nectar production was higher than 2 µl per flower (Gill and Wolf 1975). In our study, chasing was commonly observed among feeding sunbirds. A particular feeding hierarchy was observed between *C. bouvieri* and *C. reichenowi*, with the latter actively repelled from open terrain with *Lobelia columnaris* growth. In general, *C. bouvieri* was dominant during interspecific aggression events (88.6%).

Aggressive behaviour probably leads to resource partitioning between the studied sunbird species as is the case in New World hummingbirds (e.g. Feinsinger 1978; Feinsinger et al. 1985; Arizmendi 1990). The key factor determining resource partitioning between dominant and submissive competitors among nectar feeders in general is likely to be the concentration of sugar in the nectar (Wolf 1975; Carpenter and MacMillen 1976; Trombulak 1990; Lott and Lott 1991; Temeles et al. 2005). *C. bouvieri*, the dominant species in our study, mainly visited *Lobelia columnaris*, which has the second highest daily sugar content per flower, whereas the submissive *C. reichenowi* fed mostly on two plant species, each with a relatively lower daily nectar sugar content per flower (*Hypericum revolutum* or *Hypoestes aristata*).

Competition between the studied sunbird species for nectar resources was affected by their habitat preferences. *C. reichenowi* originally occupied montane forests (Cheke et al. 2001). However, due to deforestation in this mountainous region, it is now widely distributed over the mosaic of forest and open terrain habitats (Reif et al. 2007). *C. bouvieri* is primarily a species of open terrain and woodlands (Cheke et al. 2001) and has successfully colonized deforested parts of the mountains (personal observation). Although the species differ slightly in their habitat use (Reif et al. 2007), both occur in open-terrain plots overgrown by *Pteridium aquilinum* where *Lobelia columnaris* represents the only nectar resource. In contrast, *C. bouvieri* did not visit *Impatiens sakerana*, which is the most nectar-rich plant species in the study plot, with a daily sugar content even higher than that of *Lobelia columnaris* (Bartoš et al. 2009). This plant species was visited solely by *C. reichenowi*. This pattern was probably caused by the occurrence of *Impatiens sakerana* in forest-like habitats that are occupied by *C. reichenowi* but which are out of the habitat niche of *C. bouvieri*.

Our results indicate that the use of different kinds of food resources (as represented by different plant species) was the most important aspect of feeding niche partitioning between the studied sunbird species. We suggest that a temporal shift in feeding activity, which has the potential to enable coexistence of closely related bird species, did not play a significant role in our study system, as evidenced by the lack of interspecific differences in the temporal use of nectar feeding between the studied sunbirds. Patterns in daily activity and proportion of nectar feeding were similar in *C. reichenowi* and *C. bouvieri*, with the proportion of nectar feeding decreasing by a similar magnitude over the course of the breeding season in both species. We therefore also suggest that this decrease may be connected to offspring rearing during the end of our study period. Sunbirds mostly feed their offspring with insects (Cheke et al. 2001) and, in fact, both studied species focused on this food type in late December. This explanation is further supported by the fact that we recorded nest building behaviour at the beginning of the study period and young sunbirds were recorded on the study site by the end of the study period in both years (personal observation).

Distinct patterns of feeding niche partitioning between these two sunbird species were found. These patterns appear to be mediated by interspecific differences in the use of different kinds of food resources and are likely to have been driven by interspecific competition, which was observed in cases of resource overlap. However, we have no experimental data to show sunbird preferences when there is a lack of a particular plant or sunbird species (e.g. Temeles et al. 2004). For example, it is possible that *C. reichenowi* would prefer *Lobelia columnaris* when *C. bouvieri* is absent. We also have no information on how nectar resources change throughout the whole year since the data were collected only during the breeding season. Therefore, the strength of the competition and possible niche shifts in the absence of a competitor remain open questions for future research.

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