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Large dietary niche overlap of sympatric open-space foraging bats revealed by carbon and nitrogen stable isotopes

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Sympatric bats engage in various strategies for dietary niche partitioning such as different microhabitat use; however, no previous study has yet looked at potential dietary niche partitioning in mammals foraging in a space void of any physical structure. Here, we used stable isotope ratios of carbon and nitrogen to investigate if three insectivorous bats of central Thailand, *Chaerephon plicatus*, *Taphozous melanopogon* and *T. theobaldi*, partition food resources when foraging in the open space of the lower boundaries of the troposphere. We quantified the isotopic dietary niches of these species and compared niche dimensions within the guild of open-space foraging bats and between this guild and the edge-foraging bat *Hipposideros larvatus*. Our results showed that stable isotope ratios of bats differed between wet and dry seasons. Consistently, open-space foraging bat species shared a similar isotopic composition in both seasons, which contrasted that of the edge-space foraging *H. larvatus*. Isotopic niche dimensions of open-space foraging bats were smaller than those of the edge-space foraging bat. Based on isotopic data, we inferred that open-space foraging bats foraged mostly on dipterans which may fly or drift to higher altitudes where these bats hunt. In contrast, *H. larvatus* included mostly beetles from C₄ food webs in their diet, highlighting that this species is an important predator of pest insects of C₄ crops, namely cane sugar and corn. Our study emphasizes that the unstructured aerosphere in which open-space foraging bats hunt insects may promote a large overlap in the diet of these species. We conclude that mechanisms other than trophic niche differentiation, such as the motion capacity of bat species, both in terms of covered distances and accessed altitudes may facilitate the coexistence of high-altitude foraging bats.

Key words: niche width, tropical bats, diet shifts, niche overlap, diet estimation

INTRODUCTION

Sympatric bat species often differ in resource use in at least one dimension of their multi-dimensional niche space. Trophic niche partitioning is the most common mechanism by which animals partition critical resources (Schoener, 1986). It is widely assumed that bats use available microhabitats and food resources based on their wing morphology and echolocation call characteristics. Indeed, based on these two features bats can be separated roughly into seven guilds: open-space aerial, edge-space aerial, edge-space trawling, narrow-space flutter detecting, narrow-space passive gleaning, narrow-space active gleaning and narrow-space passive/active gleaning foragers (Denzinger and Schnitzler, 2013). Past studies have revealed that local insectivorous bat species, particularly closely related species, may have to differentiate in some niche dimension to

reduce competition and thus to facilitate local coexistence (Hooper and Brown, 1968). For example, Voigt and coauthors showed that congeneric rhinolophid bats from the same roost cave differed in their wing morphology which may promote different foraging styles in the same habitat and thus coexistence of the two species (Voigt *et al.*, 2010). Jiang and colleagues suggested that competition may be dampened when spatial niche differentiation may enable bats to forage in different microhabitats at the landscape level, even when species were similar in their echolocation call design (Jiang *et al.*, 2008). Recently, Roeleke and colleagues suggested that differences in the ability to cover long distances may help bat species to avoid intense competition (Roeleke *et al.*, 2018). In most cases, morphological differences in sympatric bats may lead to sufficient resource partitioning to warrant local coexistence over time (e.g., Fukui *et al.*, 2009).

Several techniques have been used to study the feeding ecology of bats, including analysis of stomach content and fecal matter by visual inspection (Leelapaibul *et al.*, 2005; Srinivasulu and Srinivasulu, 2005; Weterings *et al.*, 2015; Srilopan *et al.*, 2018), radio tracking and GPS studies (Bontadina *et al.*, 2002; Castle *et al.*, 2015; Roeleke *et al.*, 2017), direct observation (Hickey *et al.*, 1996; Acharya and Fenton, 1999) and stable isotope analysis (Rex *et al.*, 2010; Lam *et al.*, 2013; Broders *et al.*, 2014; Dammhahn and Goodman, 2014; Voigt *et al.*, 2016; Campbell *et al.*, 2017). The data obtained from both foraging observations and stomach contents has inherent biases caused by, e.g., differential digestibility of prey items, which are difficult to overcome (Kelly, 2000). Stable isotope analysis has become a widespread tool in ecological studies and is increasingly used to study animal diets over short and long time scale (Ben-David and Flaherty, 2012). This technique is based on the presumption that stable isotope ratios of an animal's body closely match that of its diet (DeNiro and Epstein, 1978, 1981). Stable carbon isotope ratios ($\delta^{13}\text{C}$) of plants differ according to the specific photosynthetic pathways used by plants (C_3 vs. C_4 plants) and thus the relevance of corresponding food webs (C_3 or C_4 plant-based food webs) for the feeding behavior of animals can be discerned from $\delta^{13}\text{C}$ values in their tissues (e.g., DeNiro and Epstein, 1978; Voigt and Kelm, 2006). Nitrogen isotopic ratios ($\delta^{15}\text{N}$) in tissues of animals increase gradually at each trophic level ($\Delta\text{N} = 2\text{--}4\text{‰}$ — DeNiro and Epstein, 1981; Vanderklift and Ponsard, 2003). Therefore, $\delta^{15}\text{N}$ values can be used to infer the trophic position of an organism (DeNiro and Epstein, 1981; Rex *et al.*, 2010; Voigt *et al.*, 2011). Further, when tissue with different isotopic retention times are considered, stable isotope ratios can be used to compare temporal and spatial variations in the diet, food web membership and foraging behavior both within and between species (DeNiro and Epstein, 1981; Sullivan *et al.*, 2006; Cryan *et al.*, 2012; Popa-Lisseanu *et al.*, 2015; Voigt *et al.*, 2016). Combining stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values may thus delineate the structure of even complex bat assemblages, particularly in those from tropical and subtropical areas (Rex *et al.*, 2010, 2011; Dammhahn and Goodman, 2014; Dammhahn *et al.*, 2015).

Most previous studies on the assemblage structure of bats have been conducted in species that forage in or around vegetation and most studies have focused on temperate zone or neotropical bat assemblages. Here, we studied the diet of four paleo-

tropical insectivorous bat species that occur in sympatry in central Thailand. Three of these species (*Chaerephon plicatus*, *Taphozous melanopogon* and *T. theobaldi*) belonged to the guild of open-space foraging bats, and one species (*Hipposideros larvatus*) belonged to the guild of edge-space foraging bats. We expected that stable isotope ratios from wing tissues will reveal guild membership because we expected species to feed on insect prey which is distinct in isotopic composition. Specifically, we hypothesized that there is a strong difference in the isotopic niches of open-space foraging bats compared to the edge-space foraging bat species. Further, we hypothesized that the three species of open-space foraging bats should forage on different prey insects in order to facilitate coexistence in the same habitat. Thus, we predicted that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and derived isotopic niche dimensions should differ between these three species. This expectation is supported by previous findings. For example, Siemers and colleagues (2011) indicated that two cryptic sibling bat species living in sympatry forage at different trophic levels enclosed by isotopic ratios. Voigt and Holderied (2012) showed that fast-flying molossid bats may encounter high metabolic costs when foraging in edge-space habitats, such as in forest gaps, forcing these bats to exploit insects in the open-space. Roswag *et al.* (2018) demonstrated strong differences in isotopic niche of a temperate gleaner bat assemblage and suggested that isotopic niche reveal the more complete picture of ecological niche. Phyllostomid bats encompass isotopically dietary spectrum across several trophic levels and forage at different stratification to partition resource available (Rex *et al.*, 2010, 2011).

MATERIALS AND METHODS

Study Species

The Horsfield's leaf-nosed bat (*Hipposideros larvatus*) is a species in the family Hipposideridae. It roosts in caves and in abandoned mines, rock crevices, mines shafts, pagodas, buildings, and tropical moist forest. Roosts are often shared with other bat species and may count up to several hundred bats (Bates *et al.*, 2008). This species has not been reported to forage at high altitude, but rather to use edge habitats, such as forest edges for hunting insects. Most of the hipposiderid bats have broad wing shapes with low wing loading and aspect ratio (Altringham, 2011) that are suitable for foraging in cluttered environments. The body mass of *H. larvatus* averages 21.5 g and forearm length 62.1 mm (Table 1; $n = 62$ — N. Ruadreo, unpublished data).

The black-bearded tomb bat (*Taphozous melanopogon*) is a species of the family Emballonuridae. This species prefers hilly and forested areas, with freshwater and roosts in caves in group of thousands of individuals (Csorba *et al.*, 2008). This

TABLE 1. Forearm length ($\bar{x} \pm SD$, in mm), body mass ($\bar{x} \pm SD$, in g) and foraging habitat of four sympatric insectivorous bat species

Species	Forearm length	Mass	Foraging habitat
<i>H. larvatus</i>	62.1 $\pm$ 2.0	21.5 $\pm$ 3.6	Forest edge/clutter
<i>T. theobaldi</i>	73.2 $\pm$ 1.8	37.9 $\pm$ 3.0	Open space
<i>T. melanopogon</i>	65.3 $\pm$ 1.3	28.6 $\pm$ 3.6	Open space
<i>C. plicatus</i>	47.1 $\pm$ 1.1	15.6 $\pm$ 1.8	Open space

species forages in open areas, through the altitudinal range at which they forage have not been reported. This species has narrow wings with high wing loading and aspect ratio. Its average body mass 28.6 g and forearm length 65.3 mm (Table 1; $n = 44$ — N. Ruadreo, unpublished data).

The Theobald's tomb bat (*Taphozous theobaldi*) is a member of the family Emballonuridae, and it is the largest representative of the genus in Thailand (Lekagul and McNeely, 1977). This species usually roosts in caves and feeds above nearby forests (Bates *et al.*, 2008). Its average body mass and forearm length are 37.9 g and 73.2 mm, respectively (Table 1; $n = 40$ — N. Ruadreo, unpublished data). Similar to other species of the genus *Taphozous*, this species has narrow wings with high wing loading and aspect ratio, and was reported to forage at high altitude of up to 800 m above ground (Roeleke *et al.*, 2017).

The wrinkle-lipped free-tailed bat (*Chaerephon plicatus*) is a species within the family Molossidae. Molossid bat usually forages at high altitudes, i.e. up to several kilometers, and as far as 25 km from their roost (Williams *et al.*, 1973). This species forms large colonies of thousands or even millions of bats in caves. Its body mass averages 15.6 g and forearm length is 47.1 mm (Table 1; $n = 42$ — N. Ruadreo, unpublished data). Their narrow wings with high wing loading and aspect ratio (Leelapaibul, 2003) identifies them a fast flying species that hunt in open space.

Study Sites and Sample Collection

We conducted our fieldwork in early May and between late July and early August 2016 representing the dry and wet seasons, respectively. Bats were captured at three caves: Wat Khao Tambon cave (15°14' N, 101°16' E — *H. larvatus* and *T. melanopogon*), Wat Tham Petch Nakha (15°08' N, 101°17' E — *H. larvatus*) and Khao Wong cave (15°02' N, 101°18' E — *T. theobaldi* and *C. plicatus* — Fig. 1). The caves are located 10–12 km to each other in the Lopburi province, central Thailand. Weather in the study site is influenced by monsoon winds with wet, dry-cool and dry seasons. The southwest monsoon starts in mid-May and ends in mid-October causing abundant rain especially during August and September. The northeast monsoon prevails over this area in mid-October to mid-February causing dry-cool weather. Pre-monsoon is the transitional period (mid-February to mid-May) from the northeast to southwest monsoons and the weather becomes dry and hot (Bua Chum meteorological station, 2016). There is usually no rain for at least five months.

There are two major land use types within 30 km of the study caves: agricultural crops (52%) and deciduous forest (48%). The agricultural landscape is dominated by two isotopically distinct crop types: C_4 crops (sugar cane (25%) and corn (6%)) and C_3 crops (rice (12%) and cassava (9%)). Each crop is grown at different times of the year. Corn is grown twice a year, yet predominantly during the wet season. Sugar cane is planted in March to June and then harvested about a year later. Cassava is cultivated all year round, it mostly grows during the early rainy season. Rice is planted in June or July and harvested from November to December.

In total, we captured 188 insectivorous bats (62 *H. larvatus*, 42 *C. plicatus*, 44 *T. melanopogon* and 40 *T. theobaldi*) with mist nets when bats emerged from the cave. From each individual, we obtained basic information such as sex, body mass (g), reproductive stage and forearm length (mm). Fur samples

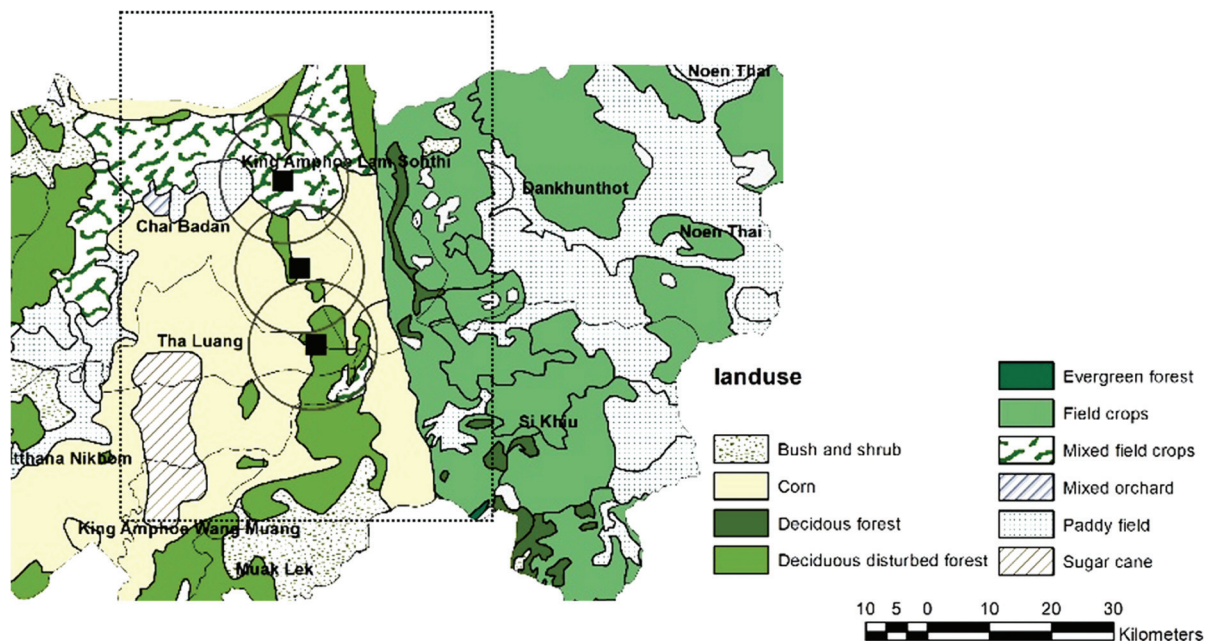


FIG. 1. Location of the study sites at Lopburi Province including Khao Tambon cave, Phet Nakha Cave and Khao Wong Cave. The 10 (circle) and 30 (dashed line square) km radius around each cave and land uses were indicated

were collected by gently cutting a small tuft of hair from the interscapular region using small scissors. Fur samples were transferred into 1.5 ml plastic vials and stored in a dry place. Further, we collected wing tissue biopsies from both membranes of the left and right wing using biopsy punches (diameter 3 mm). Wing tissue samples were dried and then stored in 1.5 ml plastic vials. After sample collection, all bats were released at the site of capture.

At night (between 18:00h and 06:00h), we collected potential insect prey groups of bats including Coleoptera, Diptera, Hemiptera and Lepidoptera (Kunz *et al.*, 1995) using modified light traps, consisting of a UV light trap equipped with a fan that sucked insects into an empty plastic detergent container. Modified light traps were within 25 km of the caves in selected habitat (rice paddies, sugar cane fields, cassava plantations and forest vegetation). A modified light trap was used in each of the four selected habitats each night for three nights in each season. All insects were separated according to trap site and stored in vials with 70% ethanol at room temperature. Samples were then dried at 50°C for 48 hours and kept dry for analyses of carbon and nitrogen stable isotope ratios.

Stable Isotopes Analyses

Prior to analysis, all samples were treated with 2: 1 chloroform: methanol solution (v/v) for 24 hours to remove lipids and external contaminants. Insect specimens were ground to small pieces. In larger insects, we selected the thorax for isotopic analysis, assuming that this body part does not deviate significantly from others with respect to isotopic composition. Afterward, samples were dried for 24 h in a drying oven at 50°C. We then used a high-precision balance to transfer 0.5 mg of each sample into separate tin capsules. All samples were analyzed by using a Flash EA 1112 Series element analyzer connected in sequence via a ConFlo to a Delta V Advantage isotope ratio mass spectrometer (all ThermoScientific, Bremen Germany). Values are reported in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ notation as parts per mille (‰) deviation from the international standard V-PDB for carbon and atmospheric nitrogen for nitrogen. The precision of analysis was better than 0.15‰ for both stable carbon and nitrogen isotope ratios.

Data Analyses and Statistical Analyses

All statistical analyses were performed with R 3.3.4 (R Core Team, 2014). We tested for seasonal and sexual variations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bat fur and wing tissues using three-way analysis of variance (three-way ANOVA). We compared isotopic niche dimensions across the four study species based on ellipsoids for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fur and wing tissue calculated

with the R-package SIBER (Jackson *et al.* 2011; Parnell and Jackson, 2013). The relative proportion of insect groups, including 95% confidence intervals in the diet of the studied bats was calculated and plotted using the mixing models from the R-package MixSIAR (Stock and Semmens, 2016). Stable isotope mixing models are used to estimate source contributions to a mixture (Phillips *et al.*, 2005; Ward *et al.*, 2011). For each model, we ran three Markov Chain Monte Carlo chains for 1,000,000 iterations with 500,000 burn in. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of bat wing tissue was used as the mixture data while $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of insect groups were used as source data to estimate the relative contribution of the specific insect group to the diet. Trophic discrimination factors (TDFs) were applied to the values of potential insect groups by adding +1‰ for C (DeNiro and Epstein, 1978) and +3‰ for N (DeNiro and Epstein 1981; Vanderklift and Ponsard, 2003) which are within the reported range observed for insectivorous bats in controlled experiments. All values are presented as means $\pm$ one standard deviation.

RESULTS

Isotopic Differences between Species, Seasons and Sexes

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fur differed across species ($\delta^{13}\text{C}$; $F_{3,174} = 184.14$, $P < 0.001$, $\delta^{15}\text{N}$; $F_{3,174} = 21.54$, $P < 0.001$), but not between seasons ($\delta^{13}\text{C}$; $F_{1,174} = 2.96$, $P > 0.05$, $\delta^{15}\text{N}$; $F_{1,174} = 0.58$, $P > 0.05$) or between sexes ($\delta^{13}\text{C}$; $F_{1,174} = 0.01$, $P > 0.05$, $\delta^{15}\text{N}$; $F_{1,174} = 1.37$, $P > 0.05$). For all pairwise comparisons among species, we observed significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($P < 0.05$), except for $\delta^{15}\text{N}$ values of *T. theobaldi* and *T. melanopogon* ($P > 0.05$ — Table 2). In wing tissue material, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values differed across bat species ($\delta^{13}\text{C}$; $F_{3,173} = 118.64$, $P < 0.001$, $\delta^{15}\text{N}$; $F_{3,173} = 14.63$, $P < 0.001$) and between seasons ($\delta^{13}\text{C}$; $F_{1,173} = 102.86$, $P < 0.001$, $\delta^{15}\text{N}$; $F_{1,173} = 19.97$, $P < 0.001$), but only $\delta^{13}\text{C}$ values differed between sexes ($\delta^{13}\text{C}$; $F_{1,173} = 5.77$, $P < 0.05$, $\delta^{15}\text{N}$; $F_{1,173} = 1.33$, $P > 0.05$). We also observed a significant interaction between species and season ($F_{3,173} = 3.03$, $P < 0.05$) and between species and sex ($F_{3,173} = 6.09$, $P < 0.05$) for $\delta^{13}\text{C}$ values. Within species, $\delta^{13}\text{C}$ values of wing tissue material were

TABLE 2. Stable carbon and nitrogen isotope ratios ($\bar{x} \pm \text{SD}$) of fur of four sympatric insectivorous bats in the dry and wet seasons, Lopburi, central Thailand. Different superscript letters indicate statistically significant differences at $P < 0.05$ (three-way ANOVA followed by Tukey test); ^{a-d} indicate statistically significant differences of $\delta^{13}\text{C}$ and ^{e-g} for $\delta^{15}\text{N}$, and *n* indicates sample sizes

Species	Dry season			Wet season		
	<i>n</i>	$\delta^{13}\text{C}_{\text{fur}}$ (‰)	$\delta^{15}\text{N}_{\text{fur}}$ (‰)	<i>n</i>	$\delta^{13}\text{C}_{\text{fur}}$ (‰)	$\delta^{15}\text{N}_{\text{fur}}$ (‰)
<i>H. larvatus</i> ^{a,c}	32	-18.1 $\pm$ 0.9	10.0 $\pm$ 0.9	30	-18.0 $\pm$ 1.0	10.1 $\pm$ 0.9
<i>T. theobaldi</i> ^{b,f}	8	-21.6 $\pm$ 1.0	10.1 $\pm$ 0.5	32	-21.1 $\pm$ 1.3	10.4 $\pm$ 0.5
<i>T. melanopogon</i> ^{c,f}	21	-22.5 $\pm$ 1.2	10.8 $\pm$ 0.4	32	-21.9 $\pm$ 0.7	10.5 $\pm$ 0.4
<i>C. plicatus</i> ^{d,g}	17	-20.4 $\pm$ 1.0	9.8 $\pm$ 0.5	25	-20.5 $\pm$ 1.0	9.4 $\pm$ 0.7

TABLE 3. Stable carbon and nitrogen isotopic ratios ($\bar{x} \pm \text{SD}$) of wing tissue of four sympatric insectivorous bats in the dry and wet seasons, Lopburi, central Thailand. Different superscript letters indicate statistically significant differences at $P < 0.05$ (three-way ANOVA followed by Tukey test); ^{a-d} indicate statistically significant differences of $\delta^{13}\text{C}$ and ^{e-f} for $\delta^{15}\text{N}$, and n indicates number of bat individuals

Species	Dry season			Wet season		
	n	$\delta^{13}\text{C}_{\text{wing}}$ (‰)	$\delta^{15}\text{N}_{\text{wing}}$ (‰)	n	$\delta^{13}\text{C}_{\text{wing}}$ (‰)	$\delta^{15}\text{N}_{\text{wing}}$ (‰)
<i>H. larvatus</i> ^e	32	-20.6 ± 1.0^e	11.1 ± 0.6	30	-19.2 ± 0.7^d	10.6 ± 0.7
<i>T. theobaldi</i> ^e	8	-23.2 ± 0.6^a	10.6 ± 0.2	32	-22.0 ± 0.6^b	10.7 ± 0.2
<i>T. melanopogon</i> ^f	21	-22.5 ± 0.6^{ab}	11.2 ± 0.5	23	-21.9 ± 0.9^{ab}	10.0 ± 0.4
<i>C. plicatus</i> ^f	17	-22.4 ± 0.6^{ab}	10.6 ± 0.4	25	-21.1 ± 0.8^c	10.2 ± 0.7

higher during the wet than during the dry season, except for *T. melanopogon* and there were no sex-specific differences in all species for $\delta^{13}\text{C}$ values, except *H. larvatus*. During the dry season, $\delta^{13}\text{C}$ values of wing tissue remained similar between *T. theobaldi*, *T. melanopogon* and *C. plicatus* ($P > 0.05$), except for *H. larvatus* which differed from all other species ($P < 0.05$). During the wet season, $\delta^{13}\text{C}$ values varied between all species, except between *T. melanopogon* and *T. theobaldi*. $\delta^{15}\text{N}$ values varied significantly among all species except between *H. larvatus* and *T. theobaldi*, and between *T. melanopogon* and *C. plicatus* ($P > 0.05$ — Table 3). $\delta^{15}\text{N}$ values of wing tissue of *H. larvatus* and *T. melanopogon* were lower in the wet than in the dry season.

Width and Overlap of Isotopic Niches

We estimated the size of the isotopic niches of the four study species by calculating a standardized ellipsoid area (SEA) based on both isotope values obtained from fur material. The ellipsoid area was corrected for small sample sizes (SEA_c). SEA_c decreased in width in the following order; *H. larvatus*, *T. theobaldi*, *C. plicatus* and *T. melanopogon*. SEA_c inferred during the dry season from fur isotopic values was significantly broader for *H. larvatus* than for the other species. Also, SEA_c of *T. theobaldi* was

significantly broader than that of *T. melanopogon* in the wet season. SEA_c inferred from wing tissue material was similar between seasons, yet differed across species (sorted according to decreasing values): *H. larvatus*, *T. melanopogon*, *C. plicatus* and *T. theobaldi* (Fig. 2). SEA_c from wing tissue of *H. larvatus* was significantly broader than that of *T. theobaldi*, *C. plicatus* and *T. melanopogon* while SEA_c of *T. melanopogon* was significantly broader than that of *T. theobaldi* in the dry season. In the wet season, SEA_c of *H. larvatus* was significantly broader than that of *T. theobaldi*.

SEA_c estimated from fur material during the dry season for *H. larvatus* and *T. melanopogon* did not overlap with that of other species. SEA_c during the wet season for *H. larvatus* and *C. plicatus* did not overlap with those of other species (Fig. 3). For wing tissue, only *H. larvatus* showed no overlap of SEA_c with any of the other species in the dry and wet season. By contrast, SEA_c of *T. theobaldi*, *T. melanopogon* and *C. plicatus* overlapped at various extents (Fig. 4).

Consumed Insect Groups Inferred from Stable Isotope Ratios

Overall, mixing models based on stable isotope ratios of wing tissue indicated that all sympatric

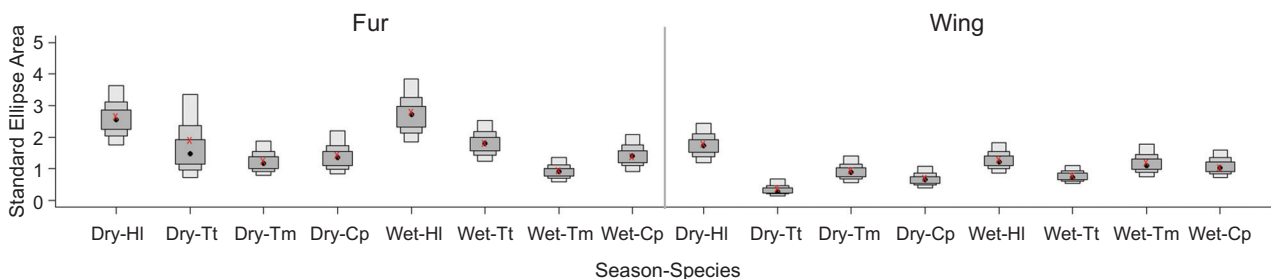


FIG. 2. Standard Ellipse Area (‰^2) of fur and wing of four sympatric insectivorous bat species in the dry and wet season (HI = *H. larvatus*, Tt = *T. theobaldi*, Tm = *T. melanopogon* and Cp = *C. plicatus*). Black dots are the mode SEA, red marks are the sample size-corrected SEA (SEA_c), boxes indicate the credible intervals (50% inside dark grey boxes, 75% middle grey boxes, and 95% outer light grey boxes) for Bayesian generated ellipses (SEA) of four sympatric insectivorous

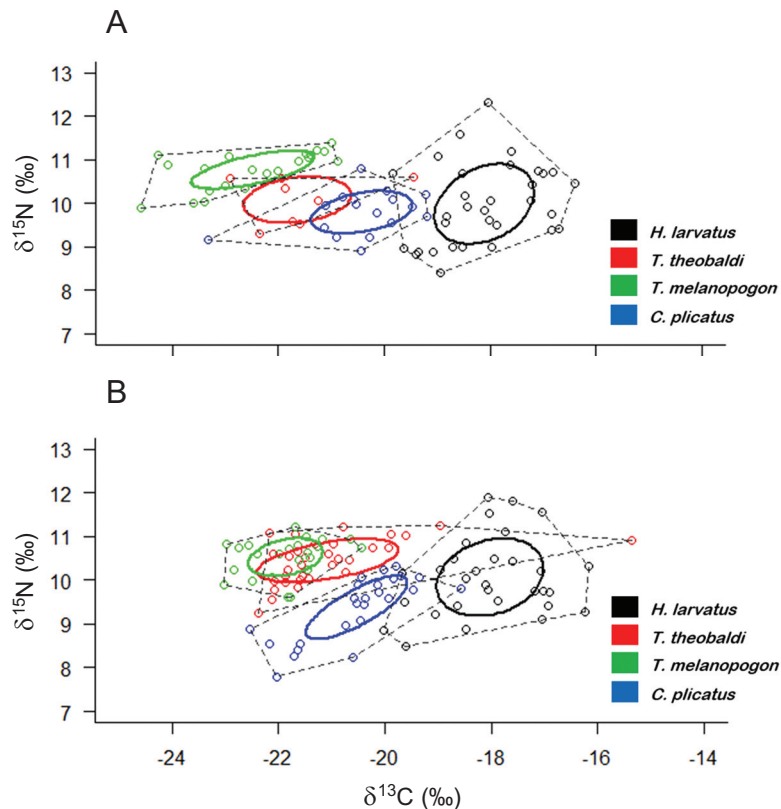


FIG. 3. Bivariate plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fur data collected from four sympatric insectivorous bat species; dashed lines represent convex hull, solid lines represent Standard Ellipse Area (SEA) in the dry (A) and wet (B) season

insectivorous bats differed in the composition of their diet during all seasons (Fig. 5). However, in a pair-wise comparison, we observed that the isotopic composition of the diet was similar in *T. theobaldi*, *T. melanopogon* and *C. plicatus*, whereas the isotopic composition of the diet of *H. larvatus* differed from all other studied species.

The diet of *H. larvatus* during the dry season consisted predominantly of Coleoptera, whereas Diptera and Lepidoptera predominated in the diet of *T. theobaldi*, and Diptera predominated in the diet of *T. melanopogon* and *C. plicatus*. The proportions changed slightly during the wet season. The diet of *H. larvatus* during the wet season consisted predominantly of Coleoptera while Diptera predominated in the diet of *T. theobaldi*, *T. melanopogon* and *C. plicatus* (Fig. 6 and Table 4).

DISCUSSION

We studied the isotopic dietary niches of four sympatric insectivorous species in central Thailand. In particular, we aimed at shedding light on the niche separation of open-space foraging bat species

that lack structural elements in their habitat, i.e. the lower boundaries of the troposphere, which might preclude the co-existence of species in the same habitat. We found that three open-space foraging bats, *C. plicatus*, *T. melanopogon* and *T. theobaldi*, share similar isotopic niche spaces when foraging high above the ground for insects. In contrast, edge-space foraging *H. larvatus* was isotopically distinct from all open-space foraging bats. Furthermore, open-space foraging bats preferred dipterans as their primary dietary source, whereas *H. larvatus* hunted mostly coleopterans.

Seasonal Variation in Tissues Isotopic Ratios, Sex-Specific Differences in Bat Species, Niche Width and Niche Overlapping

We found seasonal variations in the isotopic compositions in wing tissue material of bats, but no changes in fur samples. Seasonal variation in the diet of insectivorous bats has already been observed in other species, e.g., in bats of Madagascar (Rakotoarivelo *et al.*, 2007). We assumed that the isotopic composition of wing membrane tissue

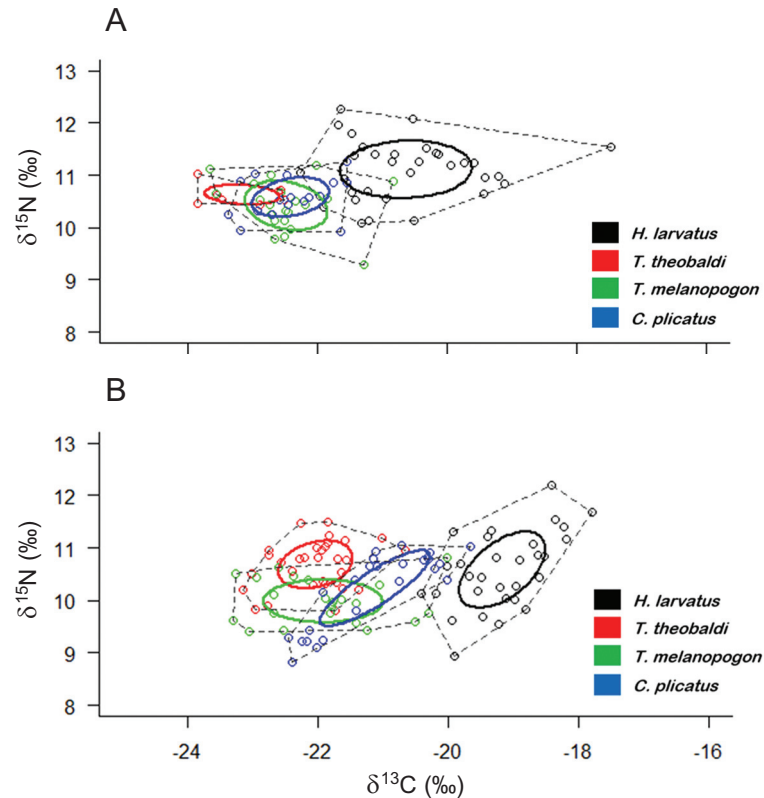


FIG. 4. Bivariate plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of wing data collected from four sympatric insectivorous bat species; dashed lines represent convex hull, solid lines represent Standard Ellipse Area (SEA) in the dry (A) and wet (B) season

integrates over the period of several weeks prior to sample collection (Voigt *et al.*, 2003; Miron *et al.*, 2006). By contrast, as an inert body product fur integrates over the isotopic composition of the diet during the time of fur growth (Cryan *et al.*, 2004;

Fraser *et al.*, 2013). Molting period in these four focal species has not been reported. Recently, we observed molting in *Taphozous theobaldi* (authors' personal observation) in May and June in this area. We also found that female *H. larvatus* consumed

TABLE 4. The proportion of potential insect groups ($\bar{x} \pm \text{SD}$) and 95% confidence interval (CI) contributing in wing tissues of four insectivorous bats in the dry and wet season

Species	Diet	Dry season		Wet season	
		$\bar{x} \pm \text{SD}$	CI	$\bar{x} \pm \text{SD}$	CI
<i>H. larvatus</i>	Coleoptera	0.45 ± 0.09	0.27–0.62	0.40 ± 0.09	0.22–0.56
	Diptera	0.24 ± 0.09	0.09–0.43	0.19 ± 0.07	0.07–0.34
	Hemiptera	0.16 ± 0.05	0.07–0.26	0.34 ± 0.06	0.22–0.46
	Lepidoptera	0.15 ± 0.07	0.03–0.29	0.08 ± 0.04	0.02–0.17
<i>T. theobaldi</i>	Coleoptera	0.19 ± 0.07	0.07–0.35	0.21 ± 0.07	0.09–0.35
	Diptera	0.45 ± 0.12	0.22–0.68	0.47 ± 0.11	0.23–0.66
	Hemiptera	0.04 ± 0.02	0.01–0.08	0.10 ± 0.04	0.03–0.18
	Lepidoptera	0.32 ± 0.10	0.11–0.52	0.22 ± 0.09	0.07–0.41
<i>T. melanopogon</i>	Coleoptera	0.13 ± 0.07	0.02–0.27	0.13 ± 0.07	0.02–0.28
	Diptera	0.56 ± 0.14	0.22–0.77	0.54 ± 0.15	0.15–0.75
	Hemiptera	0.07 ± 0.03	0.02–0.14	0.17 ± 0.06	0.06–0.30
	Lepidoptera	0.25 ± 0.11	0.06–0.50	0.17 ± 0.11	0.03–0.44
<i>C. plicatus</i>	Coleoptera	0.19 ± 0.06	0.08–0.32	0.19 ± 0.06	0.08–0.32
	Diptera	0.48 ± 0.11	0.23–0.66	0.44 ± 0.11	0.18–0.61
	Hemiptera	0.09 ± 0.03	0.03–0.16	0.22 ± 0.05	0.11–0.32
	Lepidoptera	0.25 ± 0.09	0.09–0.42	0.16 ± 0.08	0.04–0.35

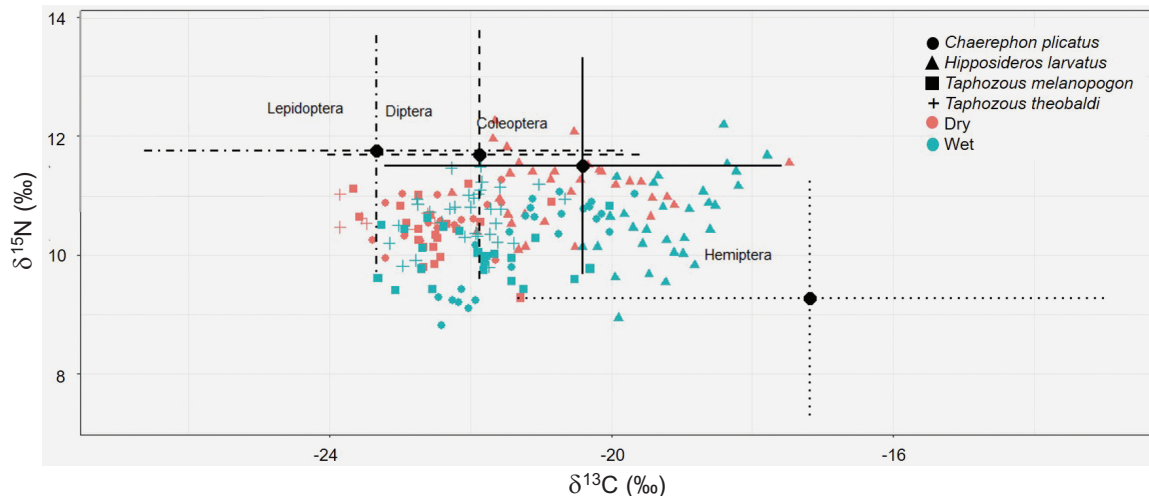


FIG. 5. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of potential prey clutters (mean $\pm$ SD) and bat wing tissue from different seasons. Prey clutters were adjusted for Trophic Discrimination Factors (cluster average + TDFs) from literature. We use +1‰ for C (DeNiro and Epstein, 1978) and +3‰ for N (DeNiro and Epstein, 1981)

insects from C_3 food web (forest) to a larger extent compared to males. This may reflect that females forage more than males in the forested area around the caves; especially during the breeding period as found in another study. *Hipposideros larvatus* gives birth to their young in late April to early May (Bu *et al.*, 2015) and female bats may require nutrient rich food to cover pregnancy and lactation (Barclay, 1985). Therefore, it seems plausible that they forage more in the nearby forests rather than to engage in long distance foraging on farmland.

Bats consumed insects at varying ratios from both food webs, i.e. food webs based on C_3 and C_4 plants. Based on $\delta^{13}\text{C}$ values, we suggested that *H. larvatus* possibly obtained and assimilated similar amounts of carbon from both food webs, while the diet of *T. theobaldi*, *T. melanopogon* and *C. plicatus* was more biased towards the C_3 food web during the dry season. During the wet season, *H. larvatus* consumed more insects from C_4 food webs than C_3 food webs, while *T. theobaldi*, *T. melanopogon* and *C. plicatus* assimilated carbon at similar rates from both food webs. In all four species, $\delta^{13}\text{C}$ values were higher during the wet season than during the dry season, indicating a predominant insect diet from the C_4 food web.

In our study, the roosting caves of *H. larvatus* are located in C_3 -dominated areas surrounded by trees and forest vegetation. The observed differences in the isotopic composition of wing tissue material may reflect seasonal changes in diet whereas the isotopic composition of the insect diet may reflect seasonal growth patterns of crop plants and natural vegetation. Increasing $\delta^{13}\text{C}$ values might indicate

a higher relevance of insects feeding on sugar cane and corn in the diet of bats during the wet season. Usually, the wet season is the period of the year when most farmers plant seedlings and when most crop plants grow. This could support larger populations of herbivorous insects during the wet season compared to the dry season. Seasonal changes in the relative contribution of insects from C_3 and C_4 food webs may also explain why isotopic niche dimension changes over time. In general, *H. larvatus* exhibited the largest isotopic niche compared to open-space foraging bats, possibly because this species depends more on insects from C_4 food webs. We found the majority of fields growing sugar cane within a 10 km radius around the cave roost of *H. larvatus*. Behavioral studies on hipposiderid species showed that this group of bats forages mostly in the understorey, such as in gap or structure edges with a high flexibility in the specific habitats used (Pavey *et al.*, 2001), yet this species group seems to avoid open areas above farmland. Thus, we assume that individuals of *H. larvatus* may have either consumed insects from the C_4 crop plants (sugar cane and corn) at the forest edge structure or they may have even moved along hedgerows or tree rows into crop fields to hunt insects there. In contrast, aerial insectivorous bats like *Taphozous* and *Chaerephon* mostly forage at high altitude (McCracken *et al.*, 2008; Roeleke *et al.*, 2017; Voigt *et al.*, 2019), thus may depend more strongly on a subset of insect prey which has moved to higher altitudes. Accordingly, niche dimensions of these open-space foraging bats were smaller than those of *H. larvatus*. The three open space foraging bats

display large overlaps in their isotopic dietary niches. This indicated that these bats exploited similar food items. In contrast to this, a previous study has revealed gleaner foraging bats to differ in their isotopic dietary niches (Roswag *et al.*, 2018). Although open-space foraging bats of our study were largely overlapping in their isotopic dietary niches, they varied in their niche width. The smaller species of the genus *Taphozous*, i.e. *T. melanopogon*, had a broader niche width than *T. theobaldi*. This might indicate that *T. melanopogon* consumed a larger variety of food insects than *T. theobaldi*. Possibly the larger species is more restricted to

the consumption of larger prey insects (Barclay and Brigham, 1991). Furthermore, a larger body size may also constrain the aerial maneuverability of bats, which may ultimately prevent larger species from hunting small insects (Aldridge and Rautenbach, 1987).

Insect Food Sources in Four Sympatric Insectivorous Bats

The stable isotope data of the two foraging guilds, i.e. open-space foraging bats (*C. plicatus* and *T. theobaldi* and *T. melanopogon*) and edge-space

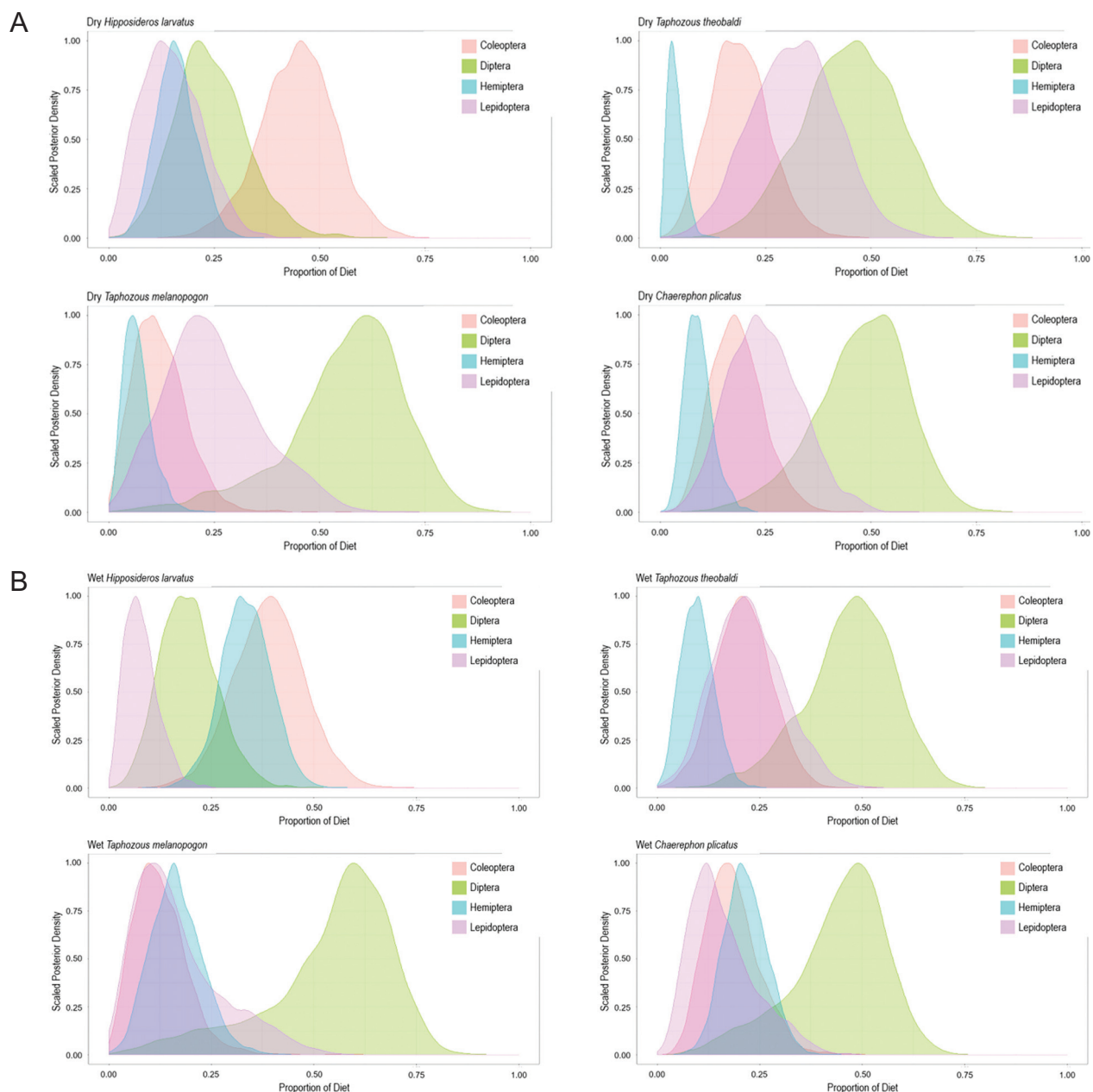


FIG. 6. The sources of diet contributing to wing tissue of four sympatric insectivorous bats in the dry (A) and wet (B) season

bats (*H. larvatus*) suggested that they differed in the insect taxa that they consumed predominantly. The major group of insects ingested by *H. larvatus* was Coleoptera. It is already known that bats that use high duty cycle echolocation such as hipposiderid bats are better able to detect glints from insect wing beats and may therefore detect the echoes of fluttering insects in the cluttered background (Kunz and Fenton, 2003; Altringham, 2011). Furthermore, hipposiderids are known to be flexible in their hunting behavior in being able to prey on airborne insects from perches or by gleaning insects from surfaces. The specific sensory ecology of this taxon makes these bats particularly well adapted to hunt beetles (Bogdanowicz *et al.*, 1999). Previous studies have already reported that the major food items of hipposiderid bats includes coleopteran, lepidopteran, dipteran and hemipteran insects (Li *et al.*, 2007; Sophia, 2010). Our isotopic data is therefore confirming previous dietary studies in hipposiderid species based on visual inspection of fecal matter.

The stable isotope data of the open-space foraging bats suggested that these species foraged predominantly on dipteran insects and that their dietary niches are large and overlapping. *Taphozous melanopogon*, *T. theobaldi* and *C. plicatus* are aerial insectivores that hunt in uncluttered areas (Bogdanowicz *et al.*, 1999; Schnitzler and Kalko, 2001; Kunz and Fenton, 2003; Altringham, 2011), and therefore, they are likely to encounter a similar set of preys. The specific wing morphology of these genera makes them particularly well adapted to hunt insects in open space (Norberg and Rayner, 1987; Voigt and Holderied, 2012). Many dipterans generally emerge at dusk and swarm over water bodies or near vegetation structures (Kunz and Fenton, 2003), possibly reaching towards higher altitudes where they are hunted by the open-space foraging bats. We assume that many of the studied bats may have hunted swarming dipterans at or closely by Pa Sak water reservoir which is the largest water body within their foraging range (25–30 km). The high percentage of dipterans in the diet of *Taphozous* corresponds well with the study of Weterings and colleagues (2015) who reported a high percentage volume of dipteran in the diet of *T. melanopogon*. However, another study revealed that this bat feeds mainly on insects of the order Coleoptera, Homoptera, and Lepidoptera when inhabiting forested habitat (Srinivasulu and Srinivasulu, 2005). Such contrasting results indicated that this bat is an opportunistic predator with a flexible hunting strategy. Recently, Roeleke *et al.* (2017) revealed that *T. theobaldi*

forages at high altitude with an average of 550 m by performing undulating altitudinal flights which correspond to the topography of the landscape. We assume that insects that occur at these altitudes are most likely of small size, which corresponds with the diet consisting predominantly of dipterans observed for this species in our study. *Chaerephon plicatus* is a specialized aerial-hawking of high-flying insects (Norberg and Rayner, 1987). Possibly, *C. plicatus* also hunt insects that migrate at higher altitudes. Small dipteran insects are known to be dispersed at high altitudes by wind (Johnson *et al.*, 1962). For example, some fruit flies were found at a range of altitude reaching from ground level to several meters or even more than 1000 m above ground (Taylor, 1960; Johnson *et al.*, 1962). In addition, coleopteran, homopteran, and lepidopteran are known to migrate at high altitudes. Therefore, we find it likely that migratory insects constitute a major part of the diet in the studied open-space bats. Consistent with this notion, Srilopan *et al.* (2018) suggested that *C. plicatus* feeds predominantly on migratory plant-hoppers during the dry season. Future studies should determine if these open space foraging bats partition in other niche dimension, such as the vertical stratum or if they prey on specific species of insects which are isotopically similar.

Our study highlights that sympatric aerial-hawking insectivorous bats share a diet with similar isotopic composition when foraging in the open space in central Thailand. The diet of *C. plicatus* and the two species of *Taphozous* included mostly dipteran insects, which might be particularly abundant at high altitude owing to their small size and the large potential of getting dispersed by wind drift. The fourth species in our study, *H. larvatus*, shows contrasting isotopic composition and patterns which implies that these bats feed more heavily on insects from C_4 food webs. Isotopic niche dimensions clearly separated *H. larvatus* from all three open-space foraging bats, which is consistent with the specific foraging habitats of these two feeding guilds. The similarity in the diet of open-space foraging bats raises the question of how species such as *C. plicatus*, *T. theobaldi* and *T. melanopogon* can coexist in the same aerial habitat when feeding on similar insect prey. We assume that other niche parameters besides insect prey may separate the niches of these three aerial insectivores. Possibly, they forage at different altitudinal ranges which are constrained by their size, morphology and physiology or they are able to detect different insect groups or size given their species-specific echolocation call design.

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