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DIET COMPOSITION AND OVERLAP IN A MONTANE FROG COMMUNITY IN VIETNAM

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Abstract.**—Southeast Asia is home to a highly diverse and endemic amphibian fauna under great threat. A significant obstacle to amphibian conservation prioritization in the region is a lack of basic biological information, including the diets of amphibians. We used stomach flushing to obtain data on diet composition, feeding strategies, dietary niche breadth, and overlap of nine species from a montane forest in Langbian Plateau, southern Vietnam: *Feihyla palpebralis* (Vietnamese Bubble-nest Frog), *Hylarana montivaga* (Langbian Plateau Frog), *Indosylvirana milleti* (Dalat Frog), *Kurixalus baliogaster* (Belly-spotted Frog), *Leptobrachium pullum* (Vietnam Spadefoot Toad), *Limnonectes poilani* (Poilane's Frog), *Megophrys major* (Anderson's Spadefoot Toad), *Polypedates* cf. *leucomystax* (Common Tree Frog), and *Raorchestes gryllus* (Langbian bubble-nest Frog). To assess food selectivity of these species, we sampled available prey in their environment. We classified prey items into 31 taxonomic groups. Blattodea was the dominant prey taxon for *K. baliogaster* whereas Coleoptera and Orthoptera were the dominant prey taxa for the other eight species. A single species, *L. pullum*, was identified as a dietary specialist feeding on Orthoptera while all other species were dietary generalists.**

Key Words.—amphibian community; diet; montane forest; Southeast Asia

INTRODUCTION

Amphibians play an important role in ecosystems at both the larval and adult stage. Larval amphibians influence the diversity and abundance of primary consumers and transfer energy from aquatic environments to the land as they metamorphose into terrestrial adults (Ranvestel et al. 2004). Adult amphibians then transfer energy from invertebrates to higher trophic levels (Burton and Likens 1975; Duellman and Trueb 1994; Wells 2007). An understanding of amphibian trophic patterns is therefore important in determining how they affect ecosystem structure and function (Ranvestel et al. 2004).

Understanding the dietary patterns of amphibian species is even more important in light of global amphibian declines. Amphibians are one of the most highly threatened groups of animals on the planet (Stuart et al. 2004), with 42% of all species threatened with extinction (International Union for the Conservation of Nature [IUCN] Species Survival Commission [SSC] Amphibian Specialist Group 2017). The feeding strategies of amphibians may inform conservation management, as species with a specialized diet, or narrow dietary niche, may be more sensitive to environmental change and therefore vulnerable to extinction (Clavel et al. 2011). At a community level, understanding trophic niches of amphibian species may help us to understand their ecological interactions and provide insight into factors that allow the coexistence of species in communities (Schoener 1974; Toft 1980; Duré et al. 2009).

Southeast Asia is home to a highly diverse and endemic amphibian fauna under great threat. Nearly one-third of all assessed species are threatened with extinction, primarily as a result of habitat loss (Rowley et al. 2010a; IUCN SSC Amphibian Specialist Group 2017). Basic information on amphibian diversity, distribution, and conservation status is limited and approximately 33% of all amphibian species assessed in the region are listed as Data Deficient (IUCN SSC Amphibian Specialist Group 2017). This lack of knowledge is a significant obstacle to conservation prioritization in the region (Rowley et al. 2010a). To date, the dietary patterns of amphibians in the region have received little attention (but see: Inger and Greenberg 1966; Kueh et al. 2010; Almeria and Nuñeza 2013; Ngo and Ngo 2014; Pamintuan and Starr 2016).

We investigated the diets and patterns of trophic niche overlap in a montane forest frog community on the

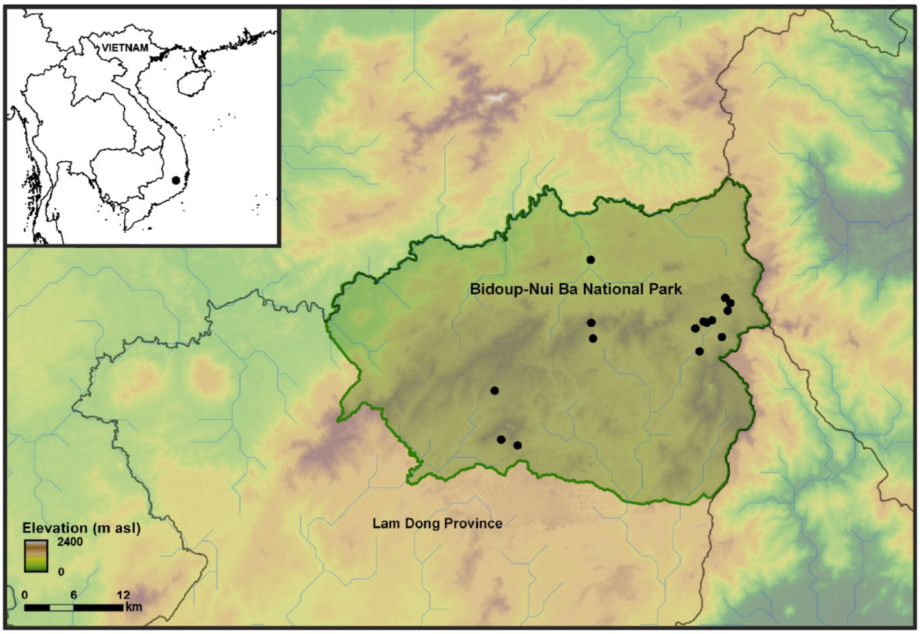

Figure 1. Location of the 15 amphibian study sites (black circles) in Bidoup-Nui Ba National Park on the Langbian Plateau, Vietnam.

Langbian Plateau, in southern Vietnam. Our knowledge of amphibian species diversity and abundance in the Plateau is unusually good for the region, as they have been the focus of much research over the last decade (Rowley et al. 2010b; Nguyen and Kuznetsov 2011; Stuart et al. 2011; Nguyen et al. 2014). The amphibian community of the area is threatened by ongoing habitat loss and modification, but our understanding of the basic biology, ecology, and dietary patterns of the frog fauna is deficient. In this study, we aimed to increase our knowledge of the dietary patterns of the frog community of the area by (1) classifying and quantifying the prey consumed by each species, (2) determining the feeding strategy (generalist or specialist) of each species, (3) estimating trophic niche breadth and niche overlap among species, and (4) assessing prey selectivity based on food availability in the environment.

Materials and Methods

Bidoup-Nui Ba National Park (NP), established in 2004, is in the southern Truong Son mountain range in Lam Dong Province, Vietnam (12.0011–12.8667°N; 108.2833–108.7291°E). The NP has a total area of 64,800 ha and ranges in altitude from 700 m to 2,200 m above sea level. Bidoup-Nui Ba NP has a subtropical climate with an average annual temperature of 18° C and average annual rainfall of 1,870 mm. There are two distinct seasons: the rainy season from April to October and the dry season from November to March (Nguyen and Kuznetsov 2011). The average relative humidity is high (84%) and varies little throughout the year (Nguyen and Kuznetsov 2011). More than 38 species of amphibians have been recorded from the NP, with a number of species thought to be endemic to the park (Nguyen and Kuznetsov 2011). Although a protected area, habitat disturbance and modification are ongoing, particularly as a result of road development and agricultural activities (Nguyen and Kuznetsov 2011).

Field surveys.—We sampled frogs in both the dry (January 2015 and 2016) and rainy (June 2015 and 2016) seasons at 15 stream sites (Fig. 1). Study streams, situated in evergreen forest above 1,000 m elevation, were about 2–4 m wide, had a permanent flow and a substrate of sand, gravel, boulders, and bedrock. The distance between study streams was at least 500 m. At each stream, we conducted nocturnal visual encounter surveys along 300 m of the stream and along two, 50-m long forest transects perpendicular to the stream, for a total of 30 forest transects. For all individuals encountered, we recorded species, sex, snout-vent length (SVL), and body mass. We determined sex by direct observation of calling, or the presence of vocal sacs, nuptial pads, or eggs. We recorded SVL to 0.1 mm using digital calipers and measured body mass using spring scales to the nearest 0.1 g (models Micro-Line 20030 or 20060; Pesola, Schindellegi, Switzerland). We used stomach flushing to obtain the stomach contents of frogs (Fraser 1976; Griffiths 1986; Leclerc and Courtois 1993; Solé et al. 2005). This method, used in herpetological studies since the 1970s (Fraser 1976), is non-lethal and provides data similar to those obtained via stomach dissection (Wu et al. 2007). In this study, we followed the protocol of Solé et al. (2005), and we flushed frogs within 3 h of capture (Legler and Sullivan 1979; Solé et al. 2005). For small frogs (< 45 mm SVL), we used 1 mm inner diameter, soft catheter tubes and a 20 ml syringe, and for large frogs (≥ 45 mm), we used 2 mm inner diameter, soft catheter tubes and a 60 ml syringe. After flushing, we released frogs at their place of capture and transferred stomach contents to 80% ethanol. As frogs were not marked, it is possible that we stomach-flushed some individuals in more than one sampling period, but the sampling interval of six months renders any repeat-sampling relatively independent.

To estimate prey availability, we carried out invertebrate trapping during frog sampling once in January and again in June 2015. Time and labor constraints prevented additional trapping. At each stream, we set up two light traps to collect flying insects, each consisting of a strip of 100 12 V light-emitting diodes (LED) glued around a 0.5 × 0.3 × 0.1 m plastic tray containing 70% ethanol (n = 30). To collect terrestrial invertebrates, we installed pitfall traps (15 cm high buckets with a diameter at the mouth of 9 cm) in triplicate at 10, 30, and 50 m along each forest transect (n = 90). Pitfall traps have been used commonly for capturing cursorial invertebrates and may be regarded as analogous to sit-and-wait predators (Cogălniceanu et al. 1998). We left light traps out for the duration of surveys (2–3 h) and left pitfall traps overnight and collected them the following morning (approximately 15 h). We preserved all arthropods collected in 80% ethanol and identified samples collected via both stomach flushing and environmental sampling to the lowest taxonomic level possible using a stereomicroscope (SZ1; Olympus, Shinjuku-ku, Tokyo, Japan) and reference keys (Ross et al. 1982; Borror et al. 1989).

Data analysis.—To evaluate the effect of season on diet, we examined only species with more than 10 individuals sampled in each season (Langbian Plateau Frog, *Hylarana montivaga*, and Common Tree Frog, *Polypedates* cf. *leucomystax*). For these two species, we used the Wilcoxon test to determine if differences exist in the frequency of occurrence and numerical proportion of prey taxa consumed between seasons using SPSS software (IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 22.0. IBM Corp, Armonk, New York, USA). Due to low sample sizes for at least one sex in each species, we combined data for males and females.

We estimated the vacuity index as the percentage of empty stomachs relative to the total number of stomachs examined (Hyslop 1980) and the intensity of feeding as the number of prey individuals per stomach. To determine whether the prey composition of each species was reliably assessed, we used a Jackknife formula to estimate the prey richness of the nine studied species with 95% confidence (Krebs 1999).

For each species, we calculated the frequency of occurrence and the numerical proportion of each prey category. We determined the frequency of occurrence (F) of each prey category by dividing the number of stomachs with prey belonging to taxonomic group X by the total number of stomachs with food. We estimated the numerical proportion (A) of each prey taxon as the number of prey belonging to taxon X divided by the total number of all prey taxa. To determine the feeding strategy of each species (specialist versus generalist), we presented food categories graphically for each species using the Costello method, modified by Amundsen et al. (Costello 1990; Amundsen et al. 1996), with the frequency of occurrence (F) on the X-axis and prey-specific abundance (PA) on the Y-axis, where PA is defined as the proportion a prey taxon comprises of all prey items in only those individuals in which this prey item occurs (Amundsen et al. 1996).

We used the numerical proportion of prey to calculate trophic niche breadth (B) using Levin's formula (Levins 1968):

$$B = \frac{1}{\sum_i^n p_i^2}$$

where *i* is the prey category, *p* is the numerical proportion of prey category *i* and *n* is the total number of prey categories. To calculate niche overlap (*O*), we used Pianka's equation (Pianka 1973):

$$O_{jk} = \frac{\sum_i^n p_{ij}\, p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

in which, p_{ij} and p_{ik} are numerical proportion of prey category *i* used by species *j* and species *k*; *n* is the total number of prey categories. To calculate selectivity in feeding, we used Ivlev's E_i index (Ivlev 1961):

$$E_i = \frac{n_i - r_i}{n_i + r_i}$$

where n_i and r_i represent the numerical proportion of prey category *i* in stomach contents and in the environment respectively. E_i can vary between -1 and 1. Prey taxa with $E_i > 0.5$ are considered preferred and those with $E_i < -0.5$ are considered avoided (Cogălniceanu et al. 1998).

Results

Diet composition.—We sampled 229 individuals of nine frog species in the study area. Species varied greatly in terms of SVL, proportion of empty stomachs, and number of prey per stomach (Table 1). Overall, 21% of all stomachs sampled were empty. Jackknife estimates suggested that more than 70% of prey

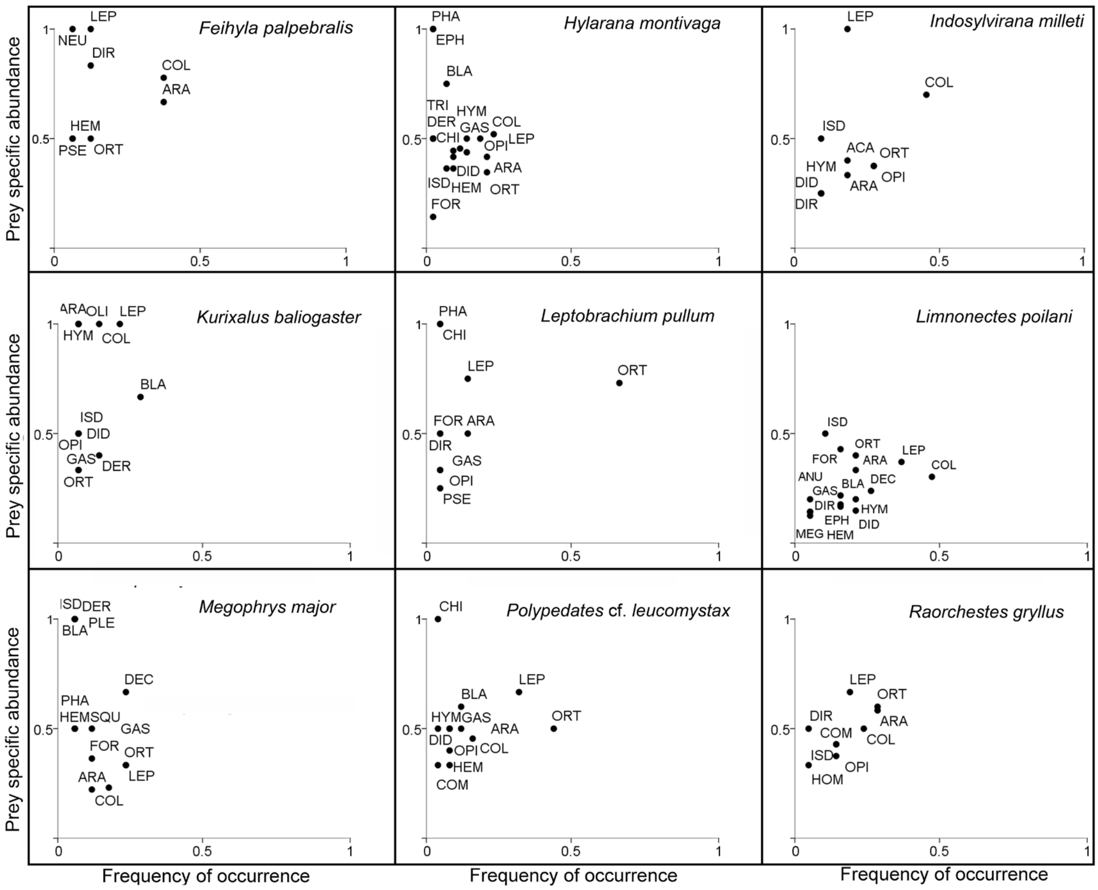

Figure 2. Costello's graphic representation (modified by Amundsen et al. 1996) showing the feeding strategies (with the frequency of occurrence on the X-axis and prey specific abundance on the Y-axis) of nine frog species in Bidoup-Nui Ba National Park, Vietnam. Abbreviations are ACA: Acarina, ANU: Anura, ARA: Aranea, BLA: Blattodea, CHI: Chilopoda, COL: Coleoptera, COM: Collembola, DEC: Decapoda, DER: Dermaptera, DID: Diplopoda, DIR: Diptera, EPH: Ephemeroptera, FOR: Formicidae, GAS: Gastropoda, HEM: Hemiptera, HOM: Homoptera, HYM: Hymenoptera, ISD: Isopoda, LEP: Lepidoptera, MEG: Megaloptera, NEU: Neuroptera, OLI: Oligochaeta, OPI: Opiliones, ORT: Orthoptera, PHA: Phasmatodea, PLE: Plecoptera, PSE: Pseudoscorpionidae, SQU: Squamata, TRI: Trichoptera.

composition was assessed in seven of the nine species (Table 1). We identified 381 prey items and classified them into 31 taxonomic groups (Appendix).

Arthropods dominated the diets of all nine species, ranging from 57% frequency of occurrence in *Limnonectes poilani* (Poilane's Frog) to 74% in *Polypedates* cf. *leucomystax*. Orthoptera, Coleoptera, Aranea, and Lepidoptera were the four main types of prey consumed by all species, except for *Leptobrachium pullum* (Vietnam Spadefoot Toad), in which Coleoptera were absent. For *L. pullum*, *Megophrys major* (Anderson's Spadefoot Toad), *P.* cf. *leucomystax*, and *Raorchestes gryllus* (Langbian Bubble-nest Frog), Orthoptera were the most frequent and abundant prey (Appendix). Coleoptera were consumed in the highest number and frequency in *Feihyla palpebralis* (Vietnamese Bubble-nest Frog), *L. poilani*, *Hylarana montivaga*, and *Indosylvirana milleti* (Dalat Frog). In *Kurixalus baliogaster* (Belly-spotted Frog), Blattodea were the most abundant and frequent prey consumed, but this group was found at low proportion or absent in the diets of remaining species (Appendix). There were no significant seasonal differences in the frequency of occurrence and numerical proportion of prey taxa for the two species with sufficient sample sizes, *Hylarana montivaga* and *Polypedates* cf. *leucomystax* (Table 2). Therefore, we pooled data for seasons and sexes in all subsequent analyses.

Feeding strategy.—For eight species (*Feihyla palpebralis*, *Hylarana montivaga*, *Indosylvirana milleti*, *Kurixalus baliogaster*, *Limnonectes poilani*, *Megophrys major*, *Polypedates* cf. *leucomystax*, and *Raorchestes gryllus*), there was an overall low frequency of occurrence of all prey categories and wide variation in specific abundance in each species, indicating a generalized feeding strategy (Fig. 2). By contrast, *Leptobrachium pullum* showed a high degree of specialization towards

Table 1. Snout-vent length (SVL) in millimeters (± standard deviation), vacuity index, number of prey per stomach, and results of Jackknife estimates for prey diversity of frog species studied in Bidoup-Nui Ba National Park, Vietnam. The number of prey per stomach was based on number of stomachs containing food. Prey categories are listed in the Appendix. The % Complete value for the Jackknife estimate of prey richness was calculated by dividing number of prey categories identified in stomach contents by the number of prey categories estimated by Jackknife formula.

Species	Male SVL	Female SVL	Total No. Analyzed Stomachs	Vacuity Index (No. Empty Stomachs)	No. Prey per Stomach (Mean ± SD)	No. Prey Categories	Jackknife Estimate of Prey Richness (% Complete)
Feihyla palpebralis	31.6 ± 7.0	34.2 ± 5.6	18	2 (11.1)	1.63 ± 0.81	8	10.81 (74)
Hylarana montivaga	49.5 ± 5.4	56.8 ± 24.0	51	7 (13.8)	1.95 ± 1.29	19	25.84 (73.6)
Indosylvirana milleti	33.6 ± 5.4	41.4 ± 8.3	14	3 (21.4)	2.18 ± 0.98	12	15.64 (76.7)
Kurixalus baliogaster	29.4 ± 2.9	37.2 ± 2.9	14	0 (0.0)	1.36 ± 0.63	12	20.43 (58.8)
Leptobrachium pullum	41.9 ± 3.9	54.1 ± 0.7	31	10 (32.3)	1.57 ± 0.87	13	21.57 (60.3)
Limnonectes poilani	69.2 ± 13.3	71.5 ± 14.7	19	0 (0.0)	4.26 ± 2.64	13	13.68 (95)
Megophrys major	58.0 ± 14.0	73.0 ± 9.2	24	7 (29.2)	1.88 ± 1.54	15	15.13 (98)
Polypedates cf. *leucomystax*	47.7 ± 14.1	59.9 ± 14.3	31	6 (19.3)	1.76 ± 0.88	13	15.88 (81.9)
Raorchestes gryllus	26.1 ± 2.9	29.9 ± 4.2	27	6 (22.2)	1.71 ± 0.90	10	11.90 (84)

Orthoptera, with other food categories consumed only occasionally (Fig. 2).

Niche breath and niche overlap.—Trophic niche breadth estimates varied greatly among species (Table 3). *Leptobrachium pullum* had the narrowest trophic niche breadth (B = 2.81) whereas *Hylarana montivaga*, *Limnonectes poilani*, and *Megophrys major* had the widest trophic niches. The average trophic niche overlap among the nine species was 0.59. The highest overlap was between *Hylarana montivga* and *Indosylvirana milleti*, with both species having a diet dominated by Coleoptera (Table 3 and Appendix).

Food selectivity.—We identified approximately 1,694 potential prey items in our traps belonging to 23 taxa (Table 4). The two most abundant prey taxa in traps, Diptera and Formicidae, appeared to be avoided by all nine species. The taxa that appear to be preferred according to Ivlev's index (Balttodea, Isopoda, and Opiliones) had low relative abundance in the traps (< 1%).

Discussion

Arthropods were the dominant prey in terms of frequency of occurrence and numerical proportion for all nine species studied. Coleoptera and Orthoptera were the dominant prey taxa for eight species: *Feihyla palpebralis*, *Hylarana montivaga*, *Indosylvirana milleti*, *Leptobrachium pullum*, *Limnonectes poilani*, *Megophrys major*, *Polypedates* cf. *leucomystax*, and *Raorchestes gryllus*. The dominance of these taxa in the diets of frogs appears to be common. Coleoptera and Orthoptera were found to be the dominant prey taxa in approximately 15 of 26 frog species studied, belonging to eight families on five continents (Cogălniceanu et al. 2000; Lima et al. 2000; Wu et al. 2005; Macale et al. 2008; Vignoli et al. 2009). Blattodea, which has not been previously reported as an important prey of frogs, were a dominant prey in *Kurixalus baliogaster*.

In this study, 21% of all stomachs were empty. Vacuity indexes in five species (*Indosylvirana milleti*, *Leptobrachium pullum*, *Megophrys major*, *Polypedates* cf. *leucomystax*, and *Raorchestes gryllus*) were higher than previous values reported (typically under 16%; Covaciu-Marcov et al. 2005; Aszalós et al. 2006; Kovács et al. 2007). However, the vacuity index is likely to change over time due to season, weather, food resource availability, and reproductive activity (Covaciu-Marcov et al. 2005; Kovács et al. 2007; Teixeira et al. 2010; Esmaeili and Johal 2015). Additional data collected over time is necessary to determine the reasons for a relatively high proportion of empty stomachs in these five species.

The only species that was identified as a dietary specialist was *Leptobrachium pullum*. This species also had the highest vacuity index. Although currently

Table 2. Results of Wilcoxon tests comparing frequency of occurrence and numerical proportion of prey taxa between wet and dry seasons for *Hylarana montivaga* and *Polypedates* cf. *leucomystax*.

	Hylarana montivaga	*Polypedates* cf. *leucomystax*
Sample size	n (dry season) = 27 n (rainy season) = 17	n (dry season) = 11 n (rainy season) = 14
Frequency of occurrence	$Z = -0.98$ $P = 0.33$	$Z = -0.33$ $P = 0.74$
Numerical proportion	$Z = -0.63$ $P = 0.53$	$Z = -0.78$ $P = 0.43$

Table 3. Trophic niche breadths of nine frog species in Bidoup-Nui Ba National Park, Vietnam, and Pianka's overlap index for each species pair based on numerical proportion of prey taxa. Genera initials are *H.* = *Hylarana*, *I.* = *Indosylvirana*, *K.* = *Kurixalus*, *L.* = *Leptobrachium; Limnonectes*, *M.* = *Megophrys*, *P.* = *Polypedates*, and *R.* = *Raorchestes*.

	Niche Breadth	*H. montivaga*	*I. milleti*	*K. baliogaster*	*L. pullum*	*L. poilani*	*M. major*	*P.* cf. *leucomystax*	*R. gryllus*
Feihyla palpebralis	5.37	0.79	0.77	0.05	0.32	0.06	0.49	0.56	0.11
Hylarana montivaga	11.52		0.87	0.70	0.50	0.84	0.64	0.80	0.85
Indosylvirana milleti	6.55			0.57	0.41	0.75	0.49	0.71	0.82
Kurixalus baliogaster	8.8				0.26	0.69	0.53	0.67	0.52
Leptobrachium pullum	2.81					0.37	0.56	0.50	0.64
Limnonectes poilani	11.51						0.80	0.72	0.67
Megophrys major	10.89							0.70	0.61
Polypedates cf. leucomystax	6.77								0.78
Raorchestes gryllus	6.97								

Table 4. Ivlev's selection index (E_i) for each prey category (taxon) for nine frog species in Bidoup-Nui Ba National Park, Vietnam. One asterisk (*) indicates preferred prey taxa ($E_i > 0.5$) and two asterisks (**) indicates avoided prey taxa ($E_i < -0.5$). Abbreviations are PA = prey abundance, Fp = *Feihyla palpebralis*, Hm = *Hylarana montivaga*, Im = *Indosylvirana milleti*, Kb = *Kurixalus baliogaster*, Lp1 = *Leptobrachium pullum*, Lp2 = *Limnonectes poilani*, Mm = *Megophrys major*, Pl = *Polypedates* cf. *leucomystax*, and Rg = *Raorchestes gryllus*.

Prey Taxon	PA	Fp	Hm	Im	Kb	Lp1	Lp2	Mm	Pl	Rg
Acarina	< 0.01	-1.00	-1.00	0.94*	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Araneae	0.06	0.58*	0.31	0.15	-0.08	0.19	0.09	0.21	0.05	0.52*
Blattodea	< 0.01	-1.00	0.87*	-1.00	0.98*	-1.00	0.93*	0.86*	0.93*	-1.00
Coleoptera	0.11	0.41	0.15	0.44	-0.03	-1.00	0.18	-0.28	0.01	0.20
Collembola	0.02	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	0.16	0.67*
Dermaptera	< 0.01	-1.00	0.60*	-1.00	0.95*	-1.00	-1.00	0.83*	-1.00	-1.00
Diplopoda	< 0.01	-1.00	0.98*	0.97*	0.98*	-1.00	0.98*	−1.00	0.97*	-1.00
Diptera	0.28	-0.18	-0.65**	-0.74**	-1.00	-0.80**	-0.91**	-1.00	-1.00	-0.82**
Ephemeroptera	0.01	-1.00	0.20	-1.00	-1.00	-1.00	0.23	-1.00	-1.00	-1.00
Formicidae	0.17	-1.00	-0.87**	-1.00	-1.00	-0.70**	-0.21	-0.15	-1.00	-1.00
Gastropoda	< 0.01	-1.00	0.97*	-1.00	0.98*	0.96*	0.97*	0.99*	0.97*	-1.00
Hemiptera	0.01	0.50	0.56*	-1.00	-1.00	-1.00	0.48	0.41	0.56*	-1.00
Homoptera	0.03	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Hymenoptera	0.04	-1.00	0.31	-0.01	0.11	-1.00	0.27	-1.00	-0.30	-1.00
Isopoda	< 0.01	-1.00	0.97*	0.97*	0.98*	-1.00	0.98*	0.96*	-1.00	0.99*
Isoptera	< 0.01	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Lepidoptera	0.11	0.01	-0.03	0.05	0.17	-1.00	0.05	0.05	0.34	0.00
Megaloptera	< 0.01	-1.00	-1.00	-1.00	-1.00	-1.00	0.91*	-1.00	-1.00	-1.00
Opiliones	0.01	-1.00	0.84*	0.89*	0.76*	0.62*	-1.00	-1.00	0.73*	0.88*
Orthoptera	0.12	-0.20	-0.05**	0.04	-0.38	0.66*	-0.22	0.04	0.37	0.25
Phasmatodea	< 0.01	-1.00	0.66*	-1.00	-1.00	0.86*	-1.00	0.86*	-1.00	-1.00
Pseudoscorpionidae	< 0.01	0.97*	-1.00	-1.00	-1.00	0.96*	-1.00	-1.00	-1.00	-1.00
Trichoptera	0.02	-1.00	-0.31	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00

considered Least Concern on the IUCN Red List of Threatened Species (IUCN SSC Amphibian Specialist Group 2017), largely as a result of its relatively widespread distribution, the species is dependent on evergreen forest, which is under great threat. Our results indicating dietary specialization (Clavel et al. 2011) suggest the species may be sensitive to environmental change.

Each of the nine studied frog species preferred different prey taxa according to our estimates of selectivity. Differences in food resource selection among species may decrease competition and allow the coexistence of species (Putman 1994). In this study, *Hylarana montivaga* and *Limnonectes poilani*, and *H. montivaga* and *Indosylvirana milleti* displayed highly overlapping diets ($O > 0.80$) but they differed from each other with regards to preferred prey types. By contrast, *I. milleti* and *Raorchestes gryllus* had a high degree of dietary overlap ($O = 0.82$) and similar preferred prey types. As *R. gryllus* is a small, arboreal species and *I. milleti* is a medium-sized, terrestrial species, differences in microhabitat and/or body/gape size and prey size choice may explain their ability to coexist (Toft 1981; Caldwell and Vitt 1999; Cogălniceanu et al. 2000). Isoptera (termites) were collected in traps but not found in stomachs of any species. This may indicate that all study species avoid termites; however, termites have been recorded in the stomach contents of at least four frog species in Southeast Asia (Inger and Greenberg 1966; Ngo and Ngo 2014). Further research is needed to make conclusions regarding selectivity of termites in our study species.

This study provides the first information on the dietary patterns of a frog community in Vietnam. Our data on feeding strategies and dietary selection of the frog species of Bidoup-Nui Ba National Park provide information useful for understanding how species coexist in tropical habitats and may be helpful in informing conservation management of amphibian species in the face of habitat loss and modification. Nonetheless, there were several limitations to our study. First, the traps we used were likely not effective for collecting all potential prey items available to frogs, and some prey found in frog stomachs (e.g., aquatic prey such as Decapoda) were not detected in the traps. Because frogs may feed in both terrestrial and aquatic habitats, future studies should use both terrestrial and aquatic traps to obtain accurate information on prey availability. Second, due to small sample sizes for most species, we were unable to examine seasonal and sex effects on dietary patterns, which are often strong (e.g., Hirai and Matsui 2000; Biavati et al. 2004; Kovács et al. 2007; Szeibel et al. 2008; Sas et al. 2009). Third, we did not analyze the relationship between body size and prey size, which may play an important role in food partitioning among species. Some prey taxa (e.g., Diptera and Ephemeroptera) were digested faster than others (e.g., Coleoptera, Decapoda, Formicidae, and Gastropoda), rendering measurements of prey size incomplete and unequal among prey taxa. Variable digestion rates among prey taxa are also why we were unable to estimate or analyze prey volumes. These limitations should be addressed in future diet studies of amphibian communities in Vietnam by increasing the number of individuals examined and the duration of study.

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Appendix. Prey categories found in stomachs of nine frog species in Bidoup-Nui Ba National Park, Vietnam. Abbreviations are n = number of specimens, A = numerical proportion, F = frequency of occurrence, and — = not recorded.

	Feihyla palpebralis n = 16		*Hylarana montivaga* n = 44		*Indosylvirana milleti* n = 11		*Kurixalus baliogaster* n = 14		*Leptobrachium pullum* n = 21		*Limnonectes poilani* n = 19		*Megophrys major* n = 17		*Polypedates* cf. *leucomystax* n = 23		*Raorchestes gryllus* n = 21	
Prey taxa	A	F	A	F	A	F	A	F	A	F	A	F	A	F	A	F	A	F
Acarina	—	—	—	—	0.08	0.18	—	—	—	—	—	—	—	—	—	—	—	—
Anura	—	—	—	—	—	—	—	—	—	—	0.01	0.06	—	—	—	—	—	—
Araneae	0.23	0.38	0.12	0.21	0.08	0.18	0.05	0.07	0.09	0.14	0.07	0.21	0.09	0.18	0.07	0.12	0.19	0.29
Blattodea	—	—	0.03	0.07	—	—	0.21	0.29	—	—	0.06	0.16	0.03	0.06	0.07	0.12	—	—
Chilopoda	—	—	0.01	0.02	—	—	—	—	0.03	0.05	—	—	—	—	0.05	0.04	—	—
Coleoptera	0.27	0.38	0.15	0.23	0.29	0.45	0.11	0.14	—	—	0.16	0.47	0.06	0.12	0.11	0.16	0.17	0.24
Collembola	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.02	0.04	0.08	0.14
Decapoda	—	—	—	—	—	—	—	—	—	—	0.06	0.26	0.13	0.24	—	—	—	—
Dermaptera	—	—	0.01	0.02	—	—	0.11	0.14	—	—	—	—	0.03	0.06	—	—	—	—
Diplopoda	—	—	0.06	0.09	0.04	0.09	0.05	0.07	—	—	0.05	0.21	—	—	0.05	0.08	—	—
Diptera	0.19	0.13	0.06	0.12	0.04	0.09	—	—	0.03	0.05	0.01	0.05	—	—	—	—	0.03	0.05
Ephemeroptera	—	—	0.01	0.02	—	—	—	—	—	—	0.01	0.05	—	—	—	—	—	—
Formicidae	—	—	0.01	0.02	—	—	—	—	0.03	0.05	0.11	0.16	0.13	0.12	—	—	—	—
Gastropoda	—	—	0.05	0.09	—	—	—	—	0.03	0.05	0.04	0.16	0.09	0.12	0.05	0.08	—	—
Hemiptera	0.04	0.06	0.05	0.07	—	—	—	—	—	—	0.04	0.16	0.03	0.06	0.05	0.08	—	—
Homoptera	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.03	0.05
Hymenoptera	—	—	0.08	0.14	0.04	0.09	0.05	0.07	—	—	0.07	0.21	—	—	0.02	0.04	—	—
Isopoda	—	—	0.05	0.09	0.04	0.09	0.05	0.07	—	—	0.06	0.11	0.03	0.06	—	—	0.08	0.14
Lepidoptera	0.12	0.13	0.10	0.19	0.13	0.18	0.16	0.21	0.09	0.14	0.12	0.37	0.13	0.24	0.23	0.32	0.11	0.19
Megaloptera	—	—	—	—	—	—	—	—	—	—	0.01	0.05	—	—	—	—	—	—
Neuroptera	0.04	0.06	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Oligochaeta	—	—	—	—	—	—	0.05	0.07	—	—	—	—	—	—	—	—	—	—
Opiliones	—	—	0.08	0.14	0.13	0.27	0.05	0.07	0.03	0.05	—	—	—	—	0.05	0.08	0.11	0.14
Orthoptera	0.08	0.13	0.10	0.21	0.13	0.27	0.05	0.07	0.58	0.67	0.07	0.21	0.13	0.24	0.25	0.44	0.19	0.29
Phasmatodea	—	—	0.01	0.02	—	—	—	—	0.03	0.05	—	—	0.03	0.06	—	—	—	—
Plecoptera	—	—	—	—	—	—	—	—	—	—	—	—	0.03	0.06	—	—	—	—
Pseudoscorpionidae	0.04	0.06	—	—	—	—	—	—	0.03	0.05	—	—	—	—	—	—	—	—
Squamata	—	—	—	—	—	—	—	—	—	—	—	—	0.03	0.06	—	—	—	—
Trichoptera	—	—	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Other	—	—	—	—	—	—	—	—	0.03	0.05	—	—	0.03	0.06	—	—	—	—