Volume 34 (July 2024), 188–196

Herpetological Journal FULL PAPER

https://doi.org/10.33256/34.3.188196

Published by the British Herpetological Society

Feeding ecology of the Jingdong frog *Odorrana jingdongensis* from Vietnam

Anh Van Pham[1], Quyen The Bui[2], Thuong Thanh Hoang[3], Hoa Thanh Thi Nguyen[3], Truong Quang Nguyen[4,5], Minh Duc Le[1,6,7] & Thomas Ziegler[8,9]

[1]Faculty of Environmental Sciences, University of Science, Vietnam National University, Ha Noi, 334 Nguyen Trai Road, Hanoi, Vietnam

[2]Mai Son High School, Son La Province, Vietnam

[3]Tay Bac University, Son La Province, Vietnam

[4]Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet Road, Cau Giay, Hanoi 10072, Vietnam

[5]Graduate University of Sience and Technology, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet Road, Cau Giay, Hanoi 10072, Vietnam

[6]Central Institute for Natural Resources and Environmental Studies, Vietnam National University, Hanoi, 19 Le Thanh Tong Street, Hanoi, Vietnam

[7]Department of Herpetology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024

[8]AG Zoologischer Garten Köln, Riehler Straße 173, D-50735 Köln, Germany

[9]Institute of Zoology, University of Cologne, Zülpicher Street 47b, D-50674 Cologne, Germany

The Jingdong frog *Odorrana jingdongensis* Fei, Ye & Li, 2001, is known from China and Vietnam. It is listed as Vulnerable in the IUCN Red list. Knowledge about natural history of this species is virtually lacking. As a result of our field work in Son La Province of north-western Vietnam, we provide novel data about the feeding ecology of *O. jingdongensis* based on stomach-flushing technique to obtain stomach contents without sacrificing the frogs, a total of 159 individuals (63 males and 96 females). We found a total of 21 prey categories with 682 items, comprising 663 items of invertebrates, three items of vertebrates and 16 unidentified items in the stomachs of *O. jingdongensis*. The most important (IRI) groups among the prey of *O. jingdongensis* were Coleoptera (32%), followed by insect larvae (11.10%), Araneae (9.60%), Orthoptera (7.49%), Hymenoptera (6.33%) and Lepidoptera (6.25%). There was an overlap of 78.16% in the diet between males and females, in both sexes the trophic spectrum was similar, predominantly consisting of Coleoptera, insect larvae, Lepidoptera, Araneae, Orthoptera and Hymenoptera. In addition, we also compared the diet composition between the three study sites and seasons. Prey categories varied from 16 to 18 in sites and were higher in the rainy season (19) compared with the dry season (16).

Keywords: amphibians, invertebrates, prey items, stomach contents, Son La Province

INTRODUCTION

Globally, one-third of all amphibian species are threatened with extinction and almost half are experiencing population declines (Stuart et al., 2004; IUCN, 2023). However, information on the diet ecology of many frogs is lacking. The diet of frogs depends on prey availability in the environment (Schoener, 1974; Toft, 1980; Strüssmann et al., 1984; Donnelly, 1991; Caldart et al., 2012; Ngo et al., 2014), so frogs in tropical-subtropical regions have more diverse diets than in temperate (Moseley et al., 2005; Ugarte et al., 2007; Hothem et al., 2009; Brito et al., 2013; Ngo et al., 2014). The main factors influencing the feeding ecology of frogs are food abundance, size constraints, ecological tolerances and climatic conditions (Toft, 1980; Duellman & Trueb, 1986; Kwet, 2001; Miranda et al., 2006). Thus the diet composition is crucial for a better understanding of the frogs' life history, population fluctuations and the impact of habitat modification on populations (Toft, 1980; Strüssmann et al., 1984; Donnelly, 1991; Ogoanah & Uchedike, 2011; Caldart et al., 2012; Merlita & Olga, 2013; Ngo et al., 2014; Pham et al., 2019a; 2022; Le et al., 2020). Mostly invertebrates and sometimes small vertebrates make up the diets of frogs, of which terrestrial and aquatic insects have been reported as preferred frog prey (Duellman & Trueb, 1994; Wells, 2007; Strüssmann et al., 1984; Miranda et al., 2006; Merlita & Olga, 2013; Ngo et al., 2014; Pham et al., 2019a; 2022; Le et al., 2020). Identifying the prey taxa for each species helps to clarify the impact of frogs on invertebrate control (Nakamura & Tominaga, 2021). Feeding is opportunistic with food up to mouth width being ingested (Donnelly, 1991; Wells, 2007; Merlita & Olga, 2013; Ngo et al., 2014). However, frogs only target moving prey and prefer elongated prey such as crickets or insect larvae that move across their field of vision (Merlita & Olga, 2013). Due to sexual dimorphism, the diet also differs between the sexes, both concerning the dietary composition or the number of prey consumed (Donnelly, 1991; Valderrama-Vernaza

Correspondence: Anh Van Pham (phamanh@hus.edu.vn)

et al., 2009; Brasileiro et al., 2010; Caldart et al., 2012). In addition, frog individuals may use different ways to find food as a response to fluctuations in prey abundance (Duellman & Trueb, 1994; Caldart et al., 2012).

The genus *Odorrana* Fei, Ye & Huang, 1990, currently contains 64 species that inhabit forest streams, from Japan, China and Indochina to India, Myanmar, Thailand, Malaya, Sumatra and Borneo (Frost, 2023). Despite the high level of species richness, dietary studies in the genus to date has only been undertaken in *O. chapaensis* and *O. morafkai* in Vietnam (Pham et al., 2019; Le et al., 2020).

The Jingdong frog *Odorrana jingdongensis* Fei, Ye & Li, 2001 was described from China. Subsequently, Bain et al. (2003) described a new species, *Rana* (*Odorrana*) *hmongorum*, with the holotype deriving from Lao Cai Province. Ohler (2007) stated that this latter species represents a junior synonym of *O. jingdongensis*. Currently, in Vietnam, *O. jingdongensis* is known from Dien Bien, Ha Giang, Lai Chau and Lao Cai provinces (Luong et al., 2021). This species is listed as Vulnerable due to over-collection and continued degradation and destruction of its habitat (IUCN SSC, 2022). This species is closely associated with forest streams in mixed secondary evergreen forest of larger and medium hardwoods, shrubs and arrowroot (Fei et al., 2001; Bain et al., 2003).

In this study, we provide information on the dietary ecology of *O. jingdongensis* for the first time.

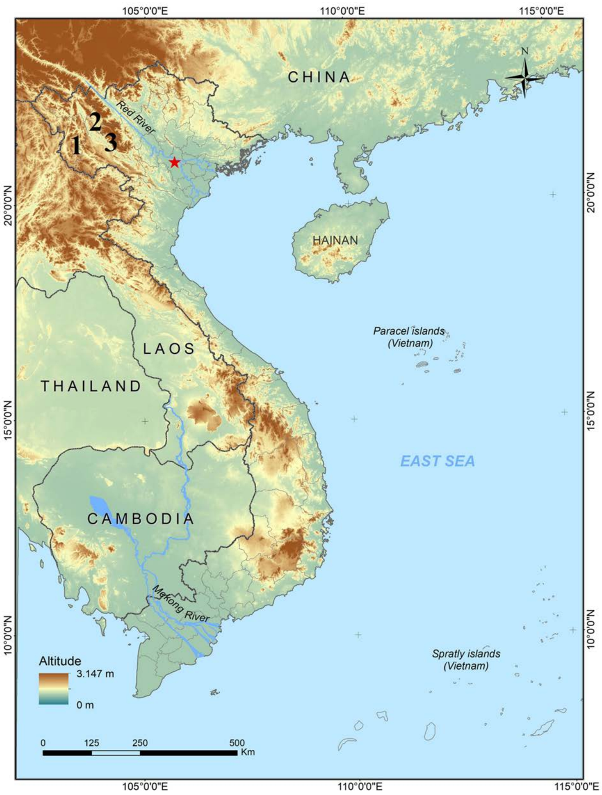

Figure 1. Map showing the survey sites in Son La Province, northern Vietnam: 1) Copia Nature Reserve; 2) Muong La Nature Reserve; and 3) Ta Xua Nature Reserve.

MATERIAL & METHODS

Field surveys were conducted in three nature reserves (NRs) of Son La Province, north-western Vietnam. The study area is characterised by a subtropical climate and seasonal monsoons with annual average rainfall ranging from 600 mm to 2000 mm, and an annual average air temperature ranging from 20 °C to 23 °C (maximum up to 40 °C and minimum -2 °C) (Nguyen, 2000). Co-ordinates were taken with a Garmin GPSMap 64SC (WGS 84 datum). Field surveys were carried out in two seasons at three sites: 1) Hua Ty Village, Co Ma Commune within Copia NR (21° 20'41.6" N, 103° 33'47.4" E, elevation 1200 m asl) from 15 to 22 April 2016 and from 13 to 16 October 2016; 2) Nam Nghiep Village, Ngoc Chien Commune within Muong La NR (21° 34'04.5" N, 104° 15'01.8" E, elevation 1580 m asl) from 26 to 30 April 2016 and from 22 to 28 October 2016, and 3) Cua Mang Village, Xim Vang Commune within Ta Xua NR (21° 20'00.2" N, 104° 25'09.9" E, elevation 1450 m asl) from 20 to 30 April 2017 (Fig. 1). The typical habitats at the three study sites were undisturbed evergreen forest, disturbed evergreen forest and secondary forest.

Frogs were collected by hand along streams transects (approximately 2.0–3.0 km in length) between the hours of 20:00 and 23:00 following the guideline approved by the American Society of Ichthyologists and Herpetologists for animal care (Beaupre et al., 2004). The surrounding habitat was mixed evergreen forest with larger and medium hardwoods, shrubs and arrowroot. The following information was recorded for each collected individual: site, date, time, elevation, temperature, relative humidity, type of vegetation and substrate type (leaf litter, moss, forest floor and leaves). Sex was determined by morphological examination based on a pair of pharyngeal subcapsular structures in males. We used a stomach-flushing technique to obtain stomach contents without sacrificing the frogs (Griffiths, 1986; Leclerc & Courtois, 1993; Solé et al., 2005). Spatula, forceps, two syringes with thread (60 ml) and the infusion tube of soft material (silicon) were used to collect prey items in the stomach of frogs, in particular for small individuals to avoid perforations of the oesophagus and stomach. Each individual was stomach-flushed only once following the guidelines approved by the American Society of Ichthyologists and Herpetologists for animal care (Beaupre et al., 2004). The water for flushing was taken from the streams where the frogs were captured and used after filtration. After stomach-flushing, frogs were monitored for vigour and body conditions and released within 30 minutes at the place of capture. Prey items were preserved in 70% ethanol. Frogs were subsequently released at the collection site after measurements of snout-vent length (SVL) and mouth width (MW) with a digital calliper to the nearest 0.01 mm and measured weight (BM) using electronic scales to the nearest 0.1 g.

Prey items were identified under a microscope (Olympus SZ 700) based on identification keys (i.e. Naumann et al., 1991; Johnson & Triplehorn, 2005; Brusca et al., 2016; Thai, 2022). The maximum length (L) and width (W) of each prey item were measured to the nearest 0.1 mm using either a caliper or a calibrated ocular micrometer fit to a microscope. The volume (V) of the prey item was calculated using the formula for a prolate spheroid (π = 3.14; Magnusson et al., 2003):

$$V = \frac{4\pi}{3} * \left(\frac{L}{2}\right) * \left(\frac{W}{2}\right)^2$$

The index of relative importance (IRI) was used to determine the importance of each food category. This index provides a more informed estimation of prey item consumption than any of the three components alone by using the following formula (Caldart et al., 2012):

$$IRI = \frac{\%F + \%N + \%V}{3}$$

where F is the frequency of prey occurrence in stomachs and N is the total number of prey items concerning all prey items.

We used the Shannon-Wiener (H) index to estimate the diversity of the diet of frogs for each site, each season and each sex category, H is calculated from the equation:

$$H = -\sum(pi * \ln(pi))$$

where pi is the ratio of food items in the taxon to the total number of food items in the sample (Magurran, 2004; Muñoz-Pedreros & Merino, 2014).

The diet overlap between males and females was calculated by measuring the percentage overlap (Krebs 1999; Caldart et al., 2012), defined by the following equation:

$$Pjk = [\sum^{n}(\text{minimum } Pij, Pik)]\ 100$$

where P_{jk} is the percentage overlap between groups j and k, P_{ij} and P_{ik} respectively represent the proportions of prey i consumed by groups j and k, and n is the total number of prey categories.

We used linear regression to examine the relationship between mouth width (MW), snout-vent length (SVL), body mass (BM) and prey size. In addition, we determined the difference between sex, sites and season.

Statistical analyses were performed with the SPSS 20.0 (SPSS Inc., Chicago, Illinois, USA) and with the significance level set to $p < 0.05$ for all analyses. Data are presented as mean ± standard deviation (SD) unless otherwise noted. We used Kendall's tau b statistics to examine the number of prey items, prey volume from frogs of different sexes, localities and season. We used one-way analysis of variance (ANOVA) to examine the size of prey items collected between sexes, among localities, and by season. We also compared the SVL and body mass of males and females using a one-way ANOVA.

RESULTS

Survey results

A total of 159 adult individuals (63 males and 96 females) of *O. Jingdongensis* were captured in Son La Province for stomach flushing, including 43 frogs from the Copia NR (19 males and 24 females); 34 from Muong La NR (15 males and 19 females); and 82 from Ta Xua NR (49 males and 33 females).

Morphological characteristics

SVL min-max: 42.0–72.5 mm; mean and SD: 56.3±7.0 mm, n=63), MW 14.4–26.7 mm (20.74 ± 2.41 mm, n=63), and body mass (BM 5.6–29.17 g, 13.98±5.5 g, n=63) in males was smaller than in females SVL 63.4–104.2 mm (82.8±10.8 mm, n=96); MW 18.0–37.1 mm (29.20±3.68 mm, n=96); BM 13.08–107.42 g, 46.24±20.22 mm, n=96) (ANOVA, all p<0.001) (Tables 1 & 2). Head longer than broad; snout round; tympanum of the males larger than in females, about two-thirds of the eye diameter; vomerine teeth developed; tongue deeply notched; discs

Table 1. Summary (Total, mean, SD and range) of the prey item number (N), width (W), length (L), and volume (V) data for *Odorrana jingdongensis* males, females and 3 communities (in mm for W and L; in mm³ for V).

			Prey item volume				
	W	L	Minimum	Maximum	Mean	Total	N
Copia (n=43)	4.83±3.62 0.50-22.0	16.02±8.77 2.0-46.0	108.80±330.15 0.33-2093.33	1130.98±1665.67 9.42-7698.80	403.20±480.28 4.0-2093.33	1723.36±2401.32 9.42-10560.34	4.07±2.30 1-9
Muong La (n=34)	3.61±1.86 0.60-12.0	11.69±6.69 2.0-42.0	34.51±48.02 0.47-226.08	393.04±479.19 29.31-2260.80	144.55±143.87 21.98-752.73	718.77±658.61 43.96-2592.07	5.38±3.42 1-15
Ta Xua (n=82)	3.44±2.20 0.5-14.0	13.33±10.22 1.0-80.0	79.56±104.50 0.26-697.08	377.05±374.34 4.71-1641.17	189.78±155.10 4.71-697.08	635.74±665.71 4.71-3496.39	3.95±6.79 1-62
Male (n=63)	2.99±2.02 0.50-10.0	10.75±8.12 1.0-46.0	66.36±104.56 0.26-697.08	291.04±272.38 4.71-1151.33	144.39±122.38 4.71-697.08	473.74±395.50 4.71-1667.08	4.38±7.78 1-62
Female (n=96)	4.42±2.83 0.5-22.0	15.49±9.32 1.90-80.0	85.37±228.31 0.33-2093.33	776.85±1211.76 9.42-7598.80	299.14±357.50 4.0-2093.33	1258.62±1761.87 9.42-10560.34	4.23±2.60 1-15
Rainy season (n=124)	3.85±2.77 0.50-22.0	14.0±9.66 1.0-80.0	91.05±211.58 0.26-2093.33	603.16±1069.07 4.71-7598.80	255.25±322.32 4.0-2093.33	965.63±1565.93 4.71-10560.34	4.06±5.72 1-62
Dry season (n=35)	3.82±2.17 0.50-12.0	12.38±7.42 2.0-42.0	31.01±33.84 0.33-157.0	517.74±601.31 29.31-2260.8	176.09±174.15 21.98-752.73	883.87±878.43 43.96-3680.77	5.09±3.18 2-15

Table 2. Results of analysis variance (ANOVA) examining the impact season, sex and sites on the number of prey items in stomachs, volume of prey, length of prey items, and width of prey items of *Odorrana jingdongensis.*

Variables	Source	df	F	*P*
Number of prey items in stomachs	Sex	1	0.027	0.869
	Sites	2	0.924	0.399
	Season	1	1.009	0.317
Volume of prey in stomachs	Sex	1	12.130	<0.001
	Sites	2	9.484	<0.001
	Season	1	0.090	0.765
Length of prey items	Sex	1	46.708	<0.001
	Sites	2	10.569	<0.001
	Season	1	4.143	0.042
Width of prey items	Sex	1	51.867	<0.001
	Sites	2	17.839	<0.001
	Season	1	0.014	0.905
SVL	Sex	1	295.189	<0.001
HW	Sex	1	247.158	<0.001
BM	Sex	1	154.736	<0.001

of fingers wide; all fingers with grooves; feet fully webbed to disks; tibiotarsal articulation reaching the tip of snout or anterior corner of eye; dorsal skin smooth, scattered with fine identical tubercles; venter smooth; dorsum olive green or dark green; dorsal limbs olive green with dark crossbars; lip-stripe yellow, indistinct, extending across upper lip; sides of body light green scattered with brown and green marks; webbing uniformly brown; venter creamy white in females and immaculate creamy white or mottled with dark brown in males. Females with white eggs and males with velvety nuptial pads on thumbs; paired gular pouches absent in males (determination after Fei et al., 2001; Bain et al., 2003; Ohler, 2007). There were strong positive correlations between the morphological measurements (SVL and MW: r=0.933, *p*< 0.001; SVL and BM: *r*=0.937; *p*<0.001; MW and body mass: *r*=0.894, *p*<0.001; Fig. 2).

Prey items

The number of prey items per individual was 1–62 (mean and SD: 4.29±5.27 items, n=159). Mean and SD prey item length was 13.58±9.15 mm (min-max: 1.0–80.0 mm, n=682); mean and SD prey item width was 3.84±2.63 mm (0.5–22.0 mm, n=682) in both sexes. The average dietary volume per individual was 947.63±1440.88 mm3 (min-max 4.71–10560.34 mm3, n=159).

There was no positive correlation between the SVL of frogs and the minimum prey volume (Kendall's_tau b=0.047, *p*=0.389) (Fig. 3a) while there were correlations between the SVL of frogs and the mean prey item volume (tau=0.216, *p*<0.001), maximum prey item volume (tau=0.262, *p*<0.001), and the total prey volume (tau=0.291, p<0.001) (Fig. 3 b,c,d). Similarly, we also found no correlation for the minimum prey volume with the MW and body mass of frogs (MW: tau=0.066, *p*=0.236, BM: tau=0.70, *p*=0.199) and there were correlations between MW and body mass of frogs with the mean prey item volume (MW: tau=0.214, *p*<0.001, BM: tau=0.225, *p*<0.001), maximum prey item volume (MW: tau=0.235, *p*<0.001, BM: tau=0.270, *p*<0.001), and the total prey volume (MW: tau=0.274, *p*<0.001, BM: tau=0.300, *p*<0.001). There were correlations between MW, BM

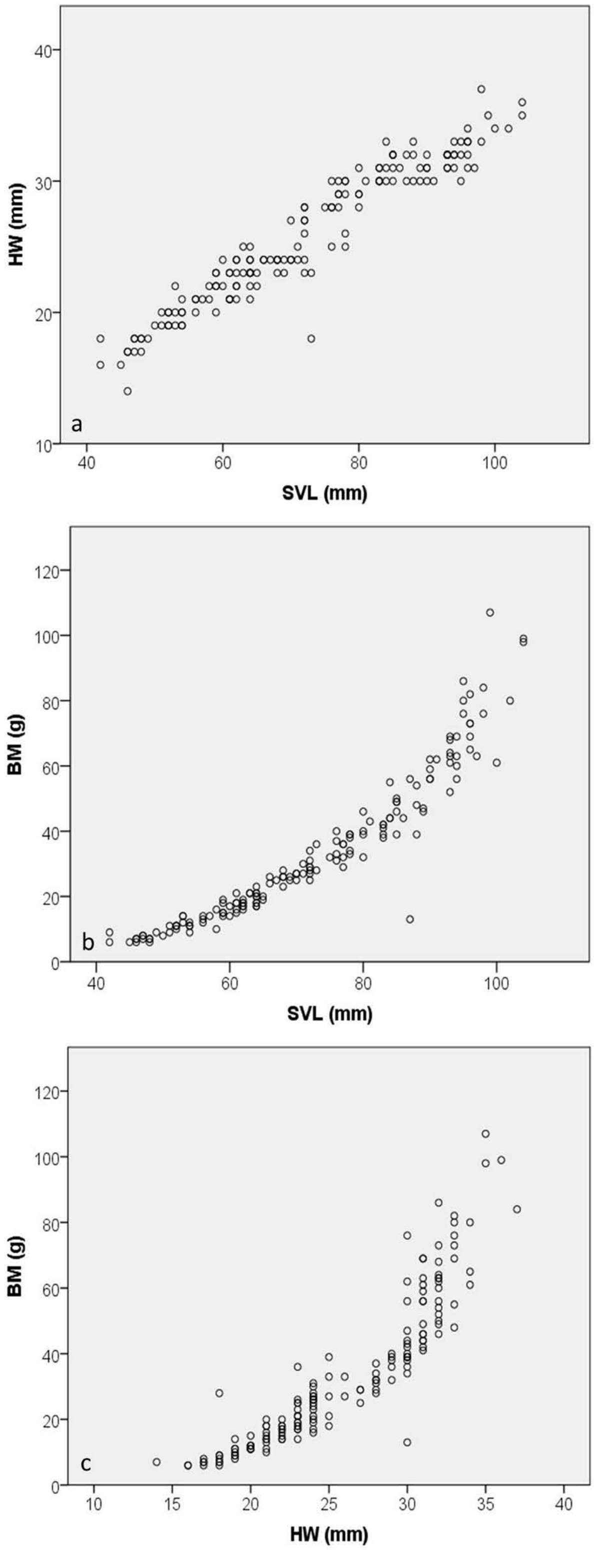

Figure 2. Dispersion diagrams from Pearson's correlations between **a)** snout-vent length and mouth width, **b)** snout-vent length and body mass, and **c)** mouth width and body mass of *Odorrana jingdongensis* in Son La Province, Vietnam.

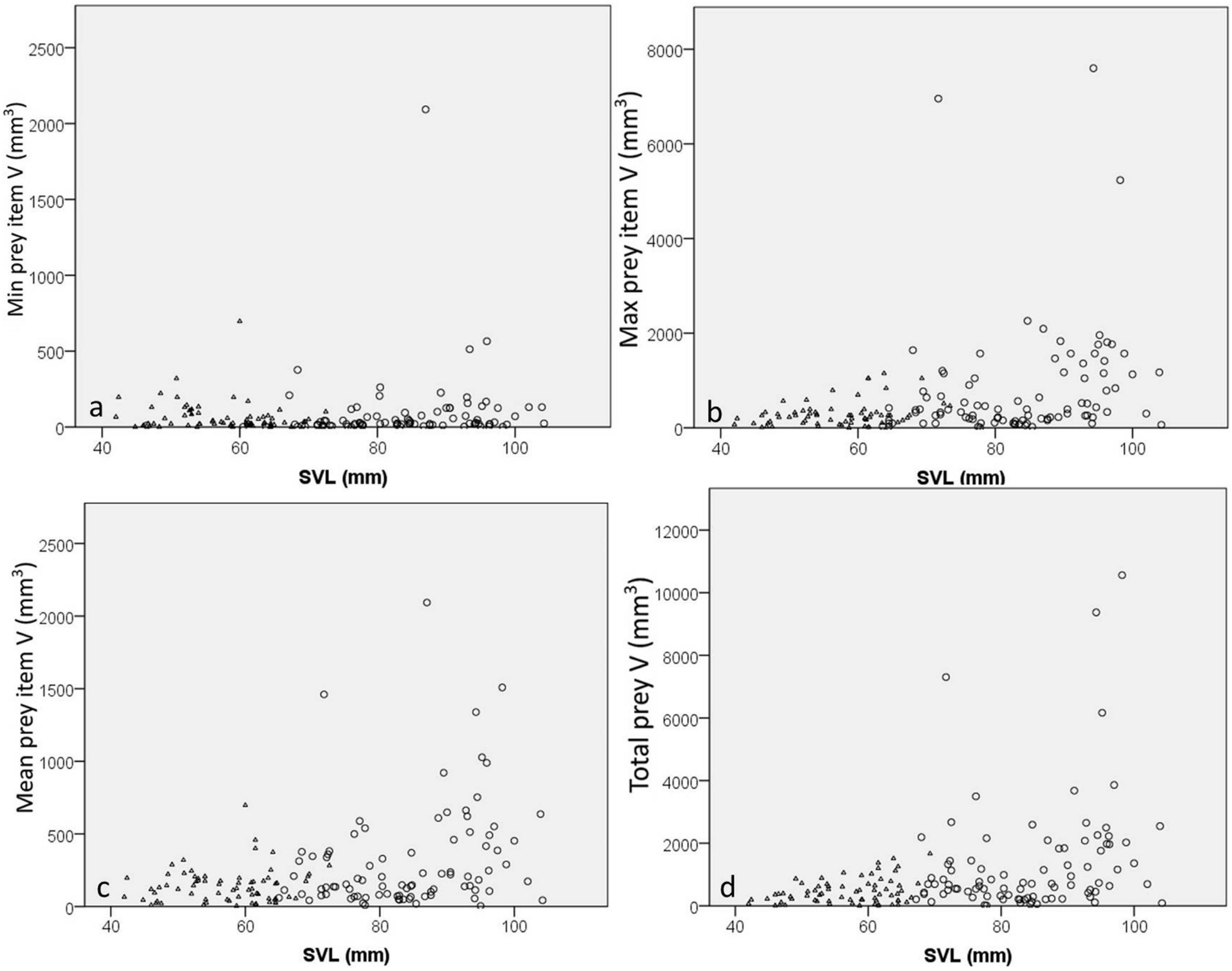

Figure 3. Relationships between the SVL of *Odorrana jingdongensis* and **a)** the minimum, **b)** maximum and **c)** the mean prey item volume, and **d)** the total prey volume. Open triangles: males; dots: females.

Table 3. Prey categories consumed by *Odorrana jingdongensis* in Son La Province, Vietnam (n=159), F) total frequency,%F) relative frequency, N) total abundance,%N) relative abundance, V) total volume (mm³),%V) relative volume; IRI) importance index.

Prey taxa	F	%F	N	%N	V	%V	IRI
Gastropoda	8	1.94	8	1.17	4,836.12	3.21	2.11
Araneae	38	9.20	43	6.30	20,013.58	13.28	9.60
Opiliones	6	1.45	7	1.03	2,383.78	1.58	1.35
Scorpiones	3	0.73	3	0.44	295.03	0.20	0.45
Polydesmida	29	7.02	31	4.55	2,038.32	1.35	4.31
Scolopendromorpha	2	0.48	2	0.29	77.45	0.05	0.28
Blattodea	9	2.18	11	1.61	9,516.82	6.32	3.37
Coleoptera	113	27.36	227	33.28	53,248.75	35.34	32.00
Dermaptera	19	4.60	26	3.81	2,943.81	1.95	3.46
Diptera	7	1.69	14	2.05	942.39	0.63	1.46
Hemiptera	10	2.42	13	1.91	1,569.74	1.04	1.79
Hymenoptera	34	8.23	58	8.50	3,376.56	2.24	6.33
Lepidoptera	29	7.02	45	6.60	7,724.66	5.13	6.25
Odonata	6	1.45	6	0.88	3,373.41	2.24	1.52
Orthoptera	32	7.75	48	7.04	11,595.99	7.70	7.49
Phasmatodea	3	0.73	3	0.44	1,196.34	0.79	0.65
Plecoptera	8	1.94	10	1.47	1,169.68	0.78	1.39
Insecta larvae	39	9.44	108	15.84	12,098.86	8.03	11.10
Amphibia	2	0.48	2	0.29	1,962.50	1.30	0.69
Reptilia	1	0.24	1	0.15	7,598.80	5.04	1.81
Unidentified	15	3.63	16	2.35	2,710.93	1.80	2.59

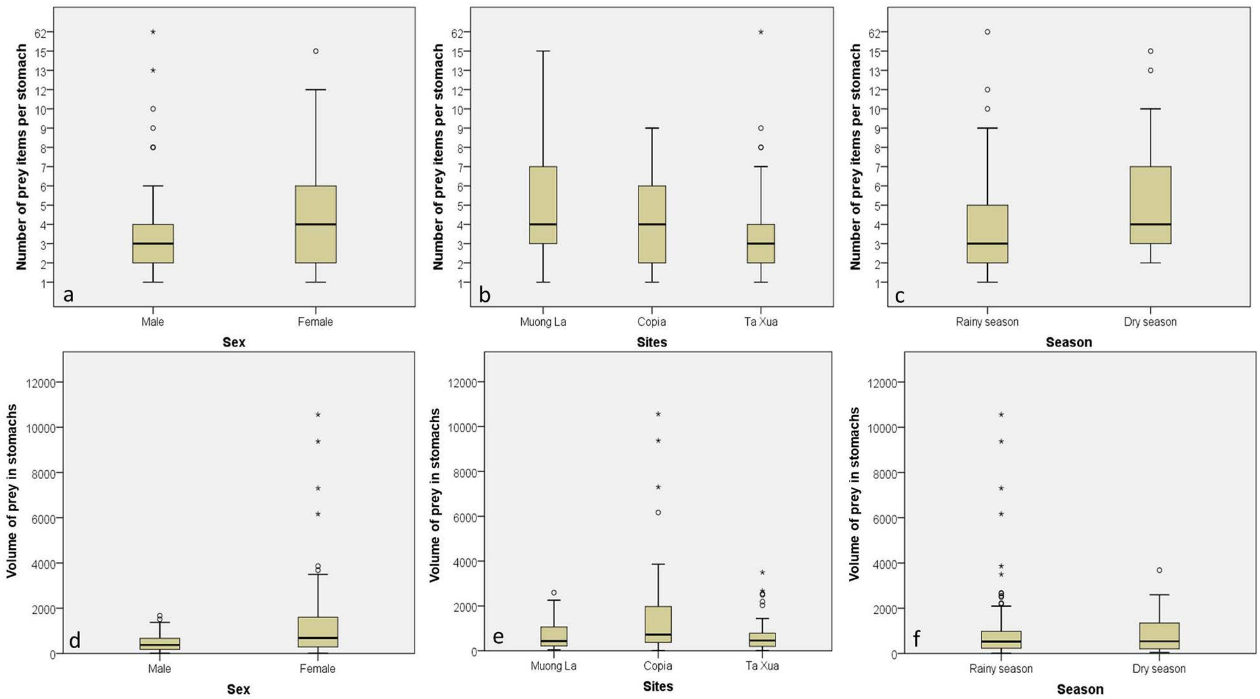

Figure 4. Boxplots representing factors that differed significantly among treatments: **a)** number of prey items of *Odorrana jingdongensis* per stomach and sex; **b)** number of prey items per stomach and sites; **c)** number of prey items per stomach and season; **d)** Prey volume per stomach and sex; **e)** prey volume per stomach and sites; **f)** prey volume per stomach and season.

and prey items: MW and width prey items: r=0.335, p<0.001; MW and length prey items: r=0.299; p<0.001; BM and width prey items: r=0.339, p<0.001; and BM and length prey items: r=0.277; p<0.001.

Dietary diversity

We identified 20 prey categories in the stomachs of *O. jingdongensis* and other unidentified objects. Insects formed the main food component of *O. jingdongensis*, with 11 orders (Blattodae, Coleoptera, Dermaptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Odonata, Orthoptera, Phasmatodea and Plecoptera) and insect larvae. Other categories were other invertebrate groups (Gastropoda, Araneae, Opiliones, Scorpiones, Polydesmida and Scolopendromorpha), Amphibia (Megophrydae) and Reptilia (Scincidae) (Table 2). The highest proportion (%N) of prey items identified was Coleoptera (32.28%), followed by insect larvae (15.84%), Hymenoptera (8.5%), Orthoptera (7.04%), Lepidoptera (6.6%), and Araneae (6.3%), while the most frequently foraged (%F) prey group was Coleoptera (27.36%), followed by insect larvae (9.44%), Araneae (9.2%), Hymenoptera (8.23%), Orthoptera (7.75%), and Lepidoptera (7.02%). In the comparisons by the IRI (%), Coleoptera (32%), followed by insect larvae (11.1%), Araneae (9.6%), Orthoptera (7.49%), Hymenoptera (6.33%), and Lepidoptera (6.25%) were found to be the most important prey groups (Table 3).

Dietary differences between sexes

The number of prey items in males was 1–62 (4.38±7.78 items, n=63) and 1–15 in females (4.23±2.6 items, n=96) (Table 1, Fig. 4a), the values were not significantly different from each other (ANOVA, $F_{1, 157}$=0.027, p=0.869) (Table 2). Mean prey item length in males were 10.75±8.12 mm (1.0–46.0 mm, n=276) and 1.9–80.0 mm in females (15.49±9.32 mm, n=406), the values were significantly different from each other ($F_{1, 680}$=46.708, p<0.001). Mean prey item width in males were 2.99±2.02 mm (0.5–10.00 mm, n=276) and ranged from 0.5 to 22.0 mm in females (4.42±2.83 mm, n=406) (Table 1), the values were also significantly different between males and females ($F_{1, 680}$=51.867, p<0.001) (Table 2). The average dietary volume per individual in males was 473.74±395.5 mm^3 (4.71–1667.08 mm^3, n=63) and 1258.62±1761.87 mm^3 (9.42–10560.34 mm^3, n=96) in females (Table 1), the values were significantly different from each other ($F_{1, 157}$=12.130, p<0.001) (Table 2, Fig. 4b).

The Shannon-Wiener index of diet diversity in *O. jingdongensis* from Son La Province was H=2.14. Adult males (19 prey categories) consumed preys with slightly lower diversity than adult females (20 prey categories). The Shannon-Wiener index of prey categories of adult males (H=2.14) was also slightly lower than that of adult females (H=2.31).

There was an overlap of 78.16% in the diet between males and females. The trophic spectrum of males with the most important (IRI>5%) consisted of Coleoptera (31.93%), insect larvae (14.33%), Lepidoptera (10.12%), Araneae (9.80%), Orthoptera (6.55%), Hymenoptera (5.77%) and Polydesmida (5.58%), while the trophic spectrum of females with the most important (IRI>5) comprised Coleoptera (32.44%), Araneae (9.53%), insect larvae (9.07%), Orthoptera (7.91%), Hymenoptera (6.63%) and Lepidoptera (5.08%) (Fig. 5).

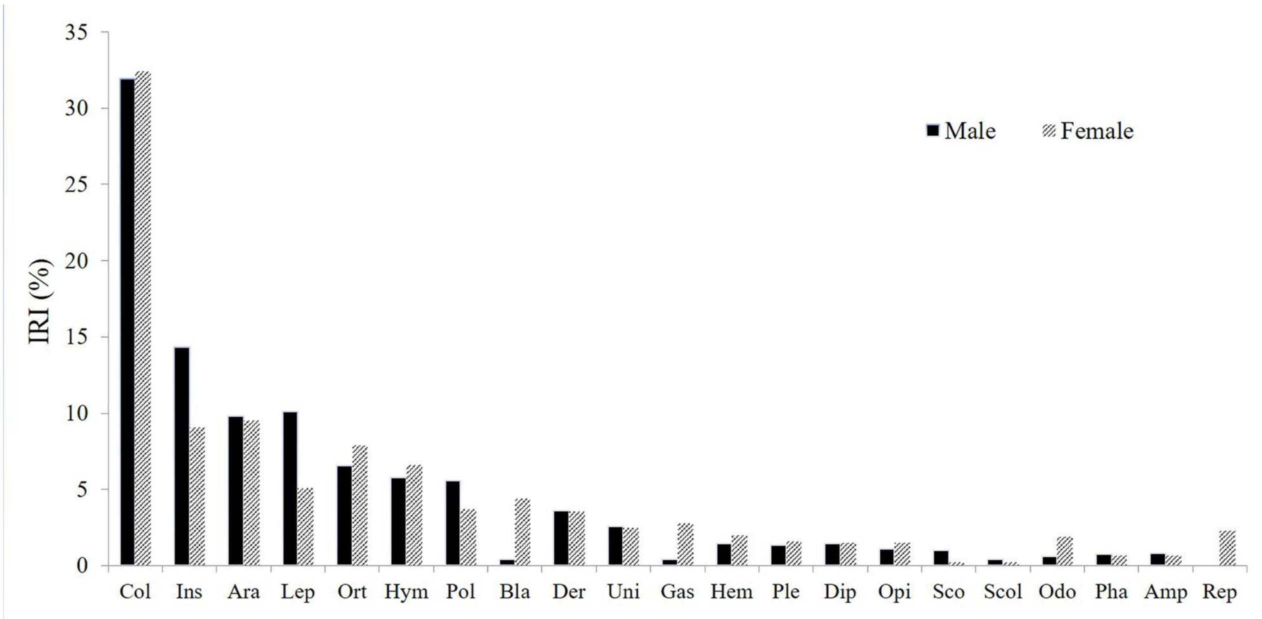

Figure 5. Importance indices (Ix) for prey categories consumed by males (black) vs. females (cross) of *Odorrana jingdongensis* in Vietnam. Coleoptera (Col), Insecta larvae (Ins), Araneae (Ara) Lepidoptera (Lep), Orthoptera (Ort), Hymenoptera (Hym), Polydesmida (Pol), Blattodea (Bla), Dermaptera (Der), Unidentified (Uni), Gastropoda (Gas), Hemiptera (Hem), Plecoptera (Ple), Diptera (Dip), Opiliones (Opi), Scorpiones (Sco), Scolopendromorpha (Scol), Odonata (Odo), Phasmatodea (Pha), Amphibia (Amp), Reptilia (Rep).

Dietary differences among sites

The number of prey items in the stomachs of frogs from Copia NR was 1–9 (4.07±2.30 items, n=43), 1–15 from Muong La NR (5.38±3.42 items, n=34), and 1–62 from Ta Xua NR (3.95±6.79 items, n=82) (Table 1, Fig. 4b), the values were not significantly different from each other ($F_{2, 156}$= 0.924, *p*=0.399) (Table 2). Mean prey item length of frogs from Copia NR was 16.02±8.77 mm (2.0–46.0 mm, n=175), 11.69±6.69 mm from Muong La NR (2.0–42.0 mm, n= 183), and 13.33±10.2 mm from Ta Xua NR (1.0–80.0 mm, n=324) (Table 1), the values were significantly different from each other ($F_{2, 680}$=10.569, *p*<0.001) (Table 2). Mean prey item width from Copia NR was 4.83±3.62 mm (0.5–22.0 mm, n=175), 3.61±1.86 mm from Muong La NR (0.6–12.0 mm, n=183), and 3.44±2.2 mm from Ta Xua NR (0.5–14.0 mm, n=324) (Table 1), the mean prey item width was significantly different between the three sites ($F_{2, 680}$=17.839, *p*<0.01) (Table 2). The average dietary volume per individual from Copia NR was 1723.36±2401.32 mm^3 (9.42–10560.34 mm^3, n=43), 718.77±658.61 from Muong La NR (43.96–2592.07 mm^3, n=34), and 635.74±665.71 mm^3 from Ta Xua NR (4.71–3496.39 mm^3, n=82) ($F_{2, 156}$=9.484, *p*<0.01) (Tables 1 & 2; Fig. 4e).

Frogs from Ta Xua NR (18 prey categories) consumed preys with a slightly higher diversity than those from Muong La NR (17 prey categories) and from Copia NR (16 prey categories). The broadest Shannon-Wiener index of diet diversity in *O. jingdongensis* was found in Muong La NR (*H*=2.41), followed by Ta Xua NR (*H*=2.1) and the narrowest dietary diversity was found in Copia NR (*H*=1.80).

Dietary differences between seasons

The number of prey items in the stomachs of frogs during the rainy season was 1–62 (4.06±5.72 items, n=124) and 2–15 during the dry season (5.09±3.18 items, n=35), the values were not significantly different from each other ($F_{1, 157}$=1.009, *p*=0.317) (Tables 1 & 2, Fig. 4c). The mean prey item length of frogs within the rainy season was 14.0±9.66 mm (1.0¬80.0 mm, n=504) and ranged from 2.0 to 42.0 mm within the dry season (12.38±7.42 mm, n=178). The mean prey item length was not significantly different between the rainy season and the dry season ($F_{1, 680}$=4.143, *p*=0.042) (Tables 1 & 2). The average dietary volume per frog individual in the rainy season was 4.71–10560.34 mm^3 (965.63±1565.93 mm^3, n=124) and 43.96–3680.77 mm^3 in the dry season (883.87±878.43 mm^3, n=35). The volume per individual was not significantly different between the rainy season and the dry season ($F_{1, 157}$=0.090, *p*=0.765) (Tables 1 & 2, Fig. 4f). The Shannon-Wiener index (*H*=2.14) of diet diversity in *O. jingdongensis* during the rainy season was lower than during the dry season (*H*=2.35), while prey categories in the rainy season (19) showed a higher diversity than during the dry season (16 prey categories).

DISCUSSION

Pham et al. (2019a) reported the dietary composition of *Odorrana chapaensis*, another representative of the genus *Odorrana* also from Muong La and Ta Xua NRs in Son La Province, Vietnam. Both *O. chapaensis* and *O. jingdongensis* inhabit similar environment conditions, viz. clinging on cliffs or tree branches near streams in mixed evergreen forests of larger and medium hardwoods and shrubs. They were found at elevations between 900 and 1600 m asl. The relative humidity was approximately 75–90% and the air temperature ranged from 20 to 30 °C. The prey categories of *O. jingdongensis* were slightly more diverse than in *O. chapaensis* (20 vs. 19

in the latter). Interestingly, the prey of *O. jingdongensis* was similar to that of *O. chapaensis*, with the prey categories Coleoptera, Hymenoptera, Orthoptera, Lepidoptera, Insecta larvae and Araneae being the most important prey items (Pham et al., 2019a). The slight differences in the diet between *O. jingdongensis* and *O. chapaensis* may reflect differences in foraging activity and microhabitat use. Scorpiones, Scolopendromorpha, Amphibia and Reptilia were found exclusively in the diet of *O. jingdongensis*, whereas Ephemeroptera, Mantodea and Trichoptera occurred only in the diet of *O. chapaensis* (Pham et al., 2019a). Prey of *O. jingdongensis* comprised mainly invertebrates but also small frogs and lizards which were not found in *O. chapaensis* (see Pham et al., 2019a).

On the other hand, the diet of *O. jingdongensis* mainly consisted of invertebrates, with Coleoptera, Hymenoptera, Orthoptera, Lepidoptera and Araneae being the most important prey categories, similar to the results found for *O. morafkai*, *Nanorana yunnanensis* and *Quasipaa verrucospinosa* (Ngo et al., 2014; Pham & Nguyen, 2018; Le et al., 2020). Beetles, which make up the main item in the diets of *O. jingdongensis*, *O. chapaensis*, *O. morafkai*, *N. yunnanensis* and *Q. verrucospinosa* are among the most abundant insects in the evergreen forest in Vietnam (Ngo et al., 2014; Pham & Nguyen, 2018; Pham et al., 2019a; Le et al., 2020). Other frog species in Vietnam have a different diet despite the dominance of beetles in the forerst ecosystem. For example, *Amolops shihaitaoi* and *Limnonectes nguyenorum* have a diet mostly consisting of ants (Pham et al., 2019b; Sonephet et al., 2023), and also some species of the family Microhylidae (*Microhyla butleri*, *M. heymonsi*) in north-western Vietnam have a diet consisting exclusively of ants and termites (Pham et al., 2022). In this study, we also found that there was very little difference in the diet composition of males and females, both sexes had a diverse prey spectrum, comprising Coleoptera, insect larvae, Lepidoptera, Araneae, Orthoptera, Hymenoptera (IRI>5%). Reptilia were found exclusively in the diet of females.

ACKNOWLEDGEMENTS

We are grateful to the directorates of Copia, Muong La and Ta Xua nature reserves for support of our field work and issuing relevant permits. We thank Sung Ba Nenh (Son La) for the assistance in the field. Field work and collection of specimens were approved by the Forest Protection Department of Son La Province (permit No. 22/GT-SL).

REFERENCES

Bain, R.H., Lathrop, A., Murphy, R.W., Orlov, N.L. & Ho, C.T. (2003). Cryptic species of a cascade frog from Southeast Asia: taxonomic revisions and descriptions of six new species. *American Museum Novitates* 3417, 1–60. http://digitallibrary.amnh.org/handle/2246/2846.

Beaupre, S.J., Jacobson, E.R., Lillywhite, H.B. & Zamudio, K. (2004). Guidelines for use of live amphibians and reptiles in feld and laboratory research. The Herpetological Animal Care and Use Commitee (HACC) of the American Society of Ichthyologists and Herpetologists. USA. 43 p.

Brasileiro, C.A., Martins, M. & Sazima, I. (2010). Feeding ecology of *Thoropa taophora* (Anura: Cycloramphidae) on a rocky seashore in southeastern Brazil. *South American Journal of Herpetology* 5(3), 181–188. https://doi.org/10.2994/057.005.0303.

Brito, L., Aguiar, F., Moura-Neto, C., Zuco, A. & Cascon, P. (2013). Diet, activity patterns, microhabitat use and defensive strategies of *Rhinella hoogmoedi* Caramaschi & Pombal, 2006 from a humid forest in northeast Brazil. *Herpetological Journal* 23, 29–37.

Brusca, R.C., Moore, W. & Shuster, S.M. (2016). Invertebrates. Oxford Univ. Press, UK. 1104 p.

Caldart, V.M., Iop, S., Bertaso, T.R.N. & Zanini, C. (2012). Feeding ecology of *Crossodactylus schmidti* (Anura: Hylodidae) in southern Brazil. *Zoological Studies* 51(4), 484–493.

Donnelly, M.A. (1991). Feeding patterns of the strawberry poison frog, *Dendrobates pumilio* (Anura: Dendrobatidae). *Copeia* 1991, 723–730. https://doi.org/10.2307/1446399.

Duellman, W.E. & Trueb, L. (1994). Biology of Amphibians. McGraw-Hill Book, USA. 670 p.

Duellman, W.E. & Trueb, L. (1986). Biology of amphibians. John Hopkins University Press, Baltimore and London. 488 p.

Griffiths, R.A. (1986). Feeding niche overlap and food selection in smooth and palmate newts, *Triturus vulgaris* and *T. helveticus*, at a pond in mid-Wales. *Journal of Animal Ecology* 55, 201–214. https://doi.org/10.2307/4702.

Fei, L., Ye, C.Y. & Li, C. (2001). Descriptions of two new species of the genus *Odorrana* in China. *Acta Zootaxonomica Sinica Beijing* 26, 108–114.

Frost, D.R. (2023). Amphibian species of the world. Accessed on 3 July 2023. http://research.amnh.org/vz/herpetology/amphibia/.

Hothem, R.L., Meckstroth, A.M., Wegner, K.E., Jennings, M.R. & Crayon, J.J. (2009). Diets of three species of anurans from the Cache Creek Watershed, California, USA. *Journal of Herpetology* 43, 275–283. https://doi.org/10.1670/06-207R1.1.

IUCN (2023). The IUCN Red List of Threatened Species. Version 2022-2. http://www.iucnredlist.org. Accessed on 1 November 2023.

IUCN SSC Amphibian Specialist Group (2022). *Odorrana jingdongensis*. The IUCN Red List of Threatened Species 2022: e.T58627A191711202. Accessed on 3 July 2023. https://dx.doi.org/10.2305/IUCN.UK.2022-2.RLTS.T58627A191711202.en.

Johnson, N.F. & Triplehorn, C.A. (2005). Borror and Delong's Introduction to the Study of Insects. Thomson Learning, Inc., California: USA. 864 p.

Krebs, C.J. (1999). Ecological Methodology. Addison Wesley Longman, Menlo Park, California, USA. 620 p.

Kwet, A. (2001). Frösche im brasilianischen Araukarienwald: Diversität, Reproduktion und Ressourcenaufteilung. Naturund-Tier-Verlag, Münster. 192 p.

Le, T.T.D., Rowley, L.J.J., Tran, T.A.D. & Hoang, D.H. (2020). The diet of a forest-dependent frog species, *Odorrana morafkai* (Anura: Ranidae), in relation to habitat disturbance.

Amphibia-Reptilia 41(1), 29–41.

Leclerc, J. & Courtois, D. (1993). A simple stomach-flushing method for ranid frogs. *Herpetological Review* 24: 142–143.

Luong, A.M., Pham, C.T., Do, H.Q., Hoang, C.V., Phan, T.Q., Nguyen Q.T., Ziegler T. & Le, M.D. (2021). New records and an updated checklist of amphibians from Lai Chau Province, Vietnam. *Check List* 17, 445–448. https://doi.org/10.15560/17.2.445.

Magnusson, W.E., Lima, A.P., Silva, W.A. & Araújo, M.C. (2003). Use of geometric forms to estimate volume of invertebrates in ecological studies of dietary overlap. *Copeia* 1, 13–19.

Magurran, A.E. (2004). Measuring biological diversity. Blackwell Science, Malden, Massachusetts, USA. *Journal of Vegetation Science* 15(6), 854–856.

Miranda, T., Ebner, M., Solé, M. & Kwet, A. (2006). Spatial, seasonal and intra polulational variation in the diet of *Pseudis cardosoi* (Anura-Hylidae) from the araucaria Plateau of Rio Grande do Sul. *Journal of Herpetology* 1(2), 121–130. https://doi.org/10.2994/1808-9798(2006)1[121:SSAIVI]2.0.CO;2.

Merlita, L.A. & Olga, M.N. (2013). Diet of seven anuran species (Amphibia: Anura) in Agusan Marsh, Mindanao, Philippines. *Animal Biology & Animal Husbandry International Journal of the Bioflux Society* 5(1), 117–126.

Moseley, K.R., Castleberry, S.B., Hanula, J.L. & Ford, W.M. (2005). Diet of southern toads (*Bufo terrestris*) in loblolly pine (*Pinus taeda*) stands subject to coarse woody debris manipulations. *American Midland Naturalist* 153, 327–337.

Muñoz-Pedreros, A. & Merino, C. (2014). Diversity of aquatic bird species in a wetland complex in southern Chile. *Journal of Natural History* 48, 1453–1465. https://doi.org/10.1080/00222933.2013.867374.

Nakamura, Y. & Tominaga, A. (2021). Diet of the American Bullfrog *Lithobates catesbeianus* Naturalized on Okinawajima, Ryukyu Archipelago, Japan. *Current Herpetology* 40(1), 40–53. https://doi.org/10.5358/hsj.40.40.

Naumann, I.D., Came, P.B., Lawrence, J.F., Nielsen, E.S., Spradbery, J.P., Taylor, R.W., Whitten., M.J. & Littlejohn, M.J. (1991). The Insects of Australia. 2 Vols, Division of Entomology, CSIRO, Australia. Melbourne University Press, Melbourne, Australia, and Cornell University Press, Ithaca, New York. 1137 p.

Ngo, V.B., Lee, Y-F. & Ngo, D.C. (2014). Variation in dietary composition of granular spiny frogs (*Quasipaa verrucospinosa*) in central Vietnam. *The Herpetological Journal* 24(3), 245–253.

Nguyen, K.V., Nguyen, T.H., Phan, K.L. & Nguyen, T.H. (2000). Bioclimatic diagrams of Vietnam, Vietnam national university publishing house, Hanoi. 64 p.

Ogoanah, O. & Uchedike, E. (2011). Diet and feeding behaviour of the edible frog *Hoplobatrachus occipitalis* (Amphibia: Anura). *African Scientist* 12(4), 209–213.

Ohler, A. (2007). New synonyms in specific names of frogs (Raninae) from the border regions between China, Laos, and Vietnam. *Alytes* 25, 55–74.

Pham, V.A., Nguyen, Q.T. & Nguyen, V.H. (2019a). Diet of *Odorrana chapaensis* (Bourret, 1937) from Son La Province. *Academia Journal of Biology* 41(3), 39–45. https://doi.org/10.15625/2615-0923/v41n3.13713.

Pham, V.A. & Nguyen, Q.T. (2018). Food spectrum of *Nanorana yunnanensis* (Anderson, 1879) from Son La Province. *Journal of Vietnam Natoinnal University Hanoi* 34(3), 10–16. https://doi.org/10.25073/2588-1140/vnunst.4747.

Pham, V.A., Nguyen, Q.T. & Nguyen V.H. (2019b). Diet of *Limnonectes nguyenorum* McLeod, Kurlbaum & Hoang from Son La Province, Vietnam. *Academia Journal of Biology* 41(2se1&2se2), 265–271.

Pham, V.A., Ngo, D.C., Nguyen, Q.T. & Ngo, V.B. (2022). Diet of *Microhyla butleri* and *M. heymonsi* from Son La Province, Northwest, Vietnam. *Herpetological Conservation and Biology* 17(1), 217–224.

Schoener, T.W. (1974). Resource partitioning in ecological communities. *Science* 185, 27–39. https://doi.org/10.1126/science.185.4145.27.

Solé, M., Beckmann, O., Pelz, B., Kwet, A. & Engels, W. (2005). Stomach-flushing for diet analysis in anurans: an improved protocol evaluated in a case study in Araucaria forests, southern Brazil. *Studies on Neotropical Fauna and Environment* 40, 23–28. https://doi.org/10.1080/01650520400025704.

Sonephet, S., Hoang, V.N., Nguyen, T.T., Nguyen, Q.T. & Pham V.A. (2023). New record and dietary ecology of a poorly known frog, *Amolops shihaitaoi* Wang, Li, Du, Hou & Yu, 2022 (Amphibia, Anura, Ranidae), from Ha Giang Province, Vietnam. *Biodiversity Data Journal* 11, e104316. https://doi.org/10.3897/BDJ.11.e104316.

Strüssmann, C., Ribeiro Do Vale M.B., Hoffmeister Meneghini, M. & Magnusson, W.E. (1984). Diet and foraging mode of *Bufo marinus* and *Leptodactylus ocellatus*. *Journal of Herpetology* 18(2), 138–146.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L. & Waller, R.W. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science* 306, 1783–1786. https://doi.org/10.1126/science.1103538.

Thai, T.B. (2022). Invertebrates. Education Publishing House, Hanoi, Vietnam. 315 p.

Toft, C.A. (1980). Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. *Oecologia* 45, 131–141.

Ugarte, C.A., Rice, K.G. & Donnelly, M.A. (2007). Comparison of diet, reproductive biology, and growth of the Pig Frog (*Rana grylio*) from harvested and protected areas of the Florida Everglades. *Copeia* 2007, 436–448. https://doi.org/10.1643/0045-8511(2007)7[436:CODRBA]2.0.CO;2.

Valderrama-Vernaza, M., Ramírez-Pinilla, M.P. & Serrano-Cardozo, V.H. (2009). Diet of the Andean frog *Ranitomeya virolinensis* (Athesphatanura: Dendrobatidae). *Journal of Herpetology* 43(1), 114–123. https://doi.org/10.1670/07-247R1.1.

Wells, K.D. (2007). The Ecology and Behavior of Amphibians. University of Chicago Press, Chicago. 1400 p.

Accepted: 8 February 2024