

Feeding Ecology of *Crossodactylus schmidtii* (Anura: Hylodidae) in Southern Brazil

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Feeding ecology of *Crossodactylus schmidtii* (Anura: Hylodidae) in southern Brazil. *Zoological Studies* 51(4): 484-493. The diet of the frog *Crossodactylus schmidtii* was studied from Sept. 2009 to Mar. 2010 in the Turvo State Park, a locality of mesophytic semideciduous forest in southern Brazil, based on 93 stomach contents obtained by stomach-flushing ($n = 80$) and analysis of preserved specimens ($n = 13$). In addition to describing the diet, we determined the niche breadth on the basis of prey categories, and calculated electivities to evaluate the relation between the diet and prey availability in the environment. We also tested for differences in diets between sexes and between adults and juveniles. *Crossodactylus schmidtii* consumed 19 categories of prey, of which ants, beetles, and dipterans had the highest importance values. Despite the varied diet, the niche breadth was narrow, with only a few prey categories being consumed predominantly. Ants, dipterans, and spiders were consumed in proportions similar to those estimated in the environment. There was no relationship between mouth width and length/volume of prey consumed, but there were significant sexual and age differences in the diet composition. Males consumed 18 prey categories, and females consumed 15; juveniles consumed 13 prey categories, and adults consumed 19. Despite differences in diet compositions between the sex and age groups, ants were the most important prey for all of them. Considering the varied diet and relationships between some of the most important items in the diet with their availability in the environment, *C. schmidtii* can be characterized as an opportunistic feeder with feeding habits similar to those of other *Crossodactylus* species. Similarities in the importance of prey items such as ants, beetles, dipterans, and insect larvae in the diet of *C. schmidtii* and other Hylodidae species are discussed. <http://zoolstud.sinica.edu.tw/Journals/51.4/484.pdf>

Key words: *Crossodactylus schmidtii*, Hylodidae, Diet, Niche breadth, Prey availability.

The diet of most anuran species is composed mainly of insects, but by consuming other invertebrates and because of the opportunistic behavior of many species, anurans are usually regarded as generalist predators (Duellman and Trueb 1994). On the other hand, some species have a narrow diet or even specialize on certain prey categories. Several species of microhylids and dendrobatids, for example, specialize on eating ants and termites (Toft 1980 1981, Donnelly 1991, Caldwell 1996,

Rödel and Braun 1999, Hirai and Matsui 2000, Solé et al. 2002). Evidence has been gathered that specialization on ants and termites by some dendrobatid species is associated with production of toxic alkaloids found in their skins (Daly et al. 1994 2002 2003, Saporito et al. 2004 2007, Darst et al. 2005). However, within the generalist-specialist continuum, there are several species that have highly varied diets, but with concentrated consumption of a few prey categories (Lima and

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Moreira 1993, Siqueira et al. 2006, Lima et al. 2010).

Anuran feeding mechanisms evolved in response to selective pressures and phylogenetic constraints, such that diets are influenced by morphology, physiology, and behavior. Prey availability of appropriate types and sizes is a factor that may also influence the diet of anurans, but few studies have assessed prey availability in the environment to allow interpretation of the results (i.e., Toft 1980 1981, Donnelly 1991, Lima and Moreira 1993). In a study on foraging habits of diurnal litter frogs and prey availability in Panama, Toft (1981) found that sit-and-wait species consume a few large prey, while active-foraging species consume small, highly mobile prey. Furthermore, individuals may use different foraging strategies as a response to fluctuations in prey abundance (Duellman and Trueb 1994).

Ontogenetic differences in the diet of frogs were studied and revealed a relationship between individual size and prey size, with individuals consuming larger prey as they grow (Donnelly 1991, Caldwell 1996, Hirai 2002, Hirai and Matsui 2002). In addition to morphological constraints, ontogenetic differences in diets were also attributed to differences in prey electivity and foraging strategies (Brasileiro et al. 2010), as well as to differences in proportions of prey consumed by different-sized individuals (Blackburn and Moreau 2006). Differences in diets may also occur between males and females, which are attributed to behavior and distinct energy expenditure between sexes (Donnelly 1991, Valderrama-Vernaza et al. 2009), or in response to seasonal variations in prey availability (Maneyro et al. 2004). As both sexes usually have the same ability to consume prey of different sizes, dietary differences between the sexes generally occur in the number of prey items consumed (Donnelly 1991, Valderrama-Vernaza et al. 2009) or in the diet composition (Brasileiro et al. 2010).

The family Hylodidae includes 42 predominantly diurnal species that inhabit forest streams, grouped in 3 genera: *Hylodes* (24 species), *Crossodactylus* (11 species), and *Megaelasia* (7 species; Frost 2011). Despite a considerable number of species, dietary studies in the family were only done on *C. aeneus* (Jordão-Nogueira et al. 2006), *C. bokermanni* (Wachlevski et al. 2008), *C. gaudichaudii*, and *Hylodes fredii* (Almeida-Gomes et al. 2007). Those studies demonstrated that these frogs have varied diets, with a high consumption of ants, beetles, dipterans, and

insect larvae. *Crossodactylus schmidti* is the only species in the *C. schmidti* group (Caramaschi and Sazima 1985), and is known only from localities of mesophytic semideciduous forest in southern Paraguay, northern Argentina, and in the Brazilian states of Paraná, Santa Catarina, and Rio Grande do Sul (Caldart et al. 2010, Lucas and Garcia 2011).

In this study, we (1) analyzed the diet of *C. schmidti* from a locality of a mesophytic semideciduous forest in southern Brazil; (2) determined the niche breadth in terms of the consumption of prey categories; (3) calculated electivities in order to evaluate relationships of the diet with prey availability in the environment; and (4) tested for differences in the diet between sexes and between adults and juveniles.

MATERIALS AND METHODS

The study was conducted in Turvo State Park (TSP), located in the municipality of Derrubadas (27°14'34.08"S, 53°57'13.74"W), northwestern Rio Grande do Sul, Brazil. TSP has an area of 17,491.4 ha and is one of the largest remnants of preserved mesophytic semideciduous forest in southern Brazil. The local climate is characterized as subtropical sub-humid with dry summer, with an annual mean temperature of 18.8°C (ST SB v type according to Maluf 2000). In the warmest month (Jan.), the mean temperature is above 22°C, and in the coldest month (July), it ranges from -3 to 18°C. Rainfall is evenly distributed throughout the year, with an annual mean of 1665 mm (SEMA 2005).

From Sept. 2009 to Mar. 2010, individuals of *C. schmidti* were collected monthly in 2 streams for a stomach-contents analysis. Stomach contents of 80 individuals were obtained through stomach-flushing to induce regurgitation (Solé et al. 2005). In addition to the contents obtained by stomach-flushing, 13 individuals collected in the same period and streams had their stomach contents analyzed. These specimens were deposited in the Herpetological Collection of the Univ. Federal de Santa Maria (vouchers ZUFMS 4587, 4673-75, 4682-84, 4686, and 4689-93).

The snout-vent length (SVL) and mouth width (MW) of individuals subjected to the stomach-contents analysis were measured with digital calipers (to an accuracy of 0.01 mm), and the mass was measured with a dynamometer (to an accuracy of 0.25 g); individuals were identified as

males, females, and juveniles. Males and females were distinguished by the presence or absence of a vocal sac, and juveniles were identified on the basis of the poor development or absence of digital spines.

Prey availability in the environment was estimated through 30 pitfall traps with a 300-ml volume, arranged along both banks of one of the streams (15 along each bank) and buried in the ground every 5 m, about 1 m from the water's edge. The traps transect covered 75 m on each side of the stream. The pitfall traps contained water and detergent, to break the water-surface tension, and were checked monthly for 3 consecutive days, from Sept. 2009 to Mar. 2010, in the same period in which stomach contents were obtained.

The diet was analyzed in terms of the occurrence, number, and volume of each prey category. Prey identification was performed at the taxonomic level of order (except at the level of family for ants), and the volume of each prey was estimated by the formula of an ovoid spheroid, proposed by Dunham (1983):

$$V = 4/3 \pi (L/2)(W/2)^2;$$

where L corresponds to the greatest length and W to the largest width of the prey. These measures were obtained from the prey dorsal surface using a camera attached to a stereomicroscope. An index of importance (I_x) was calculated for each prey category based on all stomachs examined, obtained by summing the percentage of occurrence, and the numeric and volumetric percentages of each prey in the diet, and dividing by 3. We also calculated an index of importance for prey categories based on each individual stomach, obtained by summing the numeric and volumetric percentages of each prey in the stomach, and dividing by 2.

Upon obtaining the index of importance for prey categories, we evaluated differences in diet compositions between sex and age groups (males vs. females and adults vs. juveniles) through the G test (Sokal and Rohlf 1995). We also tested for dietary changes related to the size of the prey consumed, through linear regressions between the mean length and volume of prey with the MW of individuals. To evaluate correlations among MW, SVL, and body mass, Pearson's correlations were performed. These analyses were done using BioEstat 5.0 (Ayres et al. 2007), at a significance level of $p \leq 0.05$. The sufficiency of the sample

to assess the diet composition was evaluated by an accumulation curve of prey categories, using Estimates 8.2 with 1000 random additions (Colwell 2009).

We determined the niche breadth in terms of the consumption of prey categories for species and groups (males, females, adults, and juveniles) and the diet percentage overlap between sex (males vs. females) and age groups (adults vs. juveniles), using values of the relative abundances of prey categories. Both measures were calculated using the program Ecological Methodology (Krebs 1999). The niche breadth was obtained through Levins' standardized index (Krebs 1999), in which the value of Levins' measure (B) was first obtained. Levins' measure was calculated by the following equation: $B = 1/\sum P_j^2$, where B is Levins' niche breadth measure and P_j is the fraction of item j in the diet. Levins' measure was then standardized on a scale of 0-1.0 by the following equation: $B_A = (B - 1)/(n - 1)$, where B_A corresponds to Levins' standardized niche breadth, B is Levins' niche breadth measure, and n is the number of possible resource states. Levins' standardized niche breadth ranges from 0 (the narrowest amplitude), when there is exclusive use of a single resource category, to 1 (the broadest amplitude), when all categories are equally used (Krebs 1999); the species is considered to have a wide niche breadth when $B_A \geq 0.5$. The diet overlap between groups (males vs. females and adults vs. juveniles) was calculated by measuring the percentage overlap (Krebs 1999), defined by the following equation:

$$P_{jk} = [\sum^n (\text{minimum } P_{ij}, P_{ik})] 100;$$

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.

Finally, to assess whether prey consumption by *C. schmidtii* occurred in the same proportion to prey availability in the environment, electivities were calculated using the method of Jacobs (1974), as defined by the following equation:

$$D = (d_k - f_k) / [(d_k + f_k) - (2 d_k f_k)]$$

where d_k is the proportion of prey k in the diet, and f_k is the proportion of prey k in the environment. The electivity value (D) ranges from 1, when there is selection or preference for a prey, to -1, when a prey is absent from the diet but is present in the environment. An intermediate value

(0) means that a prey is consumed at the same level as it is estimated in the environment. In this analysis, we only included prey captured in the environment that were likely to be consumed by *C. schmidti*, and excluded those that could not be preyed upon because of morphological constraints (i.e., prey the length and width of which were larger than the largest mouth width registered in *C. schmidti*, which was 11.14 mm).

RESULTS

Among 113 individuals submitted to stomach-flushing, 33 (29.2%) had no stomach contents, and 80 (70.8%) had contents. The other 13 individuals collected also had stomach contents, resulting in a total of 93 stomach contents analyzed. The diet of *C. schmidti* was composed of 19 prey categories; in addition, 2 artificial categories were created to group the contents of unidentified arthropod remains and plant remains (Table 1). The accumulation curve for prey categories showed an ascendant shape, but with a tendency

for stabilization (Fig. 1).

Prey categories that had higher importance values to the total stomach contents were Formicidae, Coleoptera and Diptera. Prey categories like Coleoptera (larvae), Araneae, and

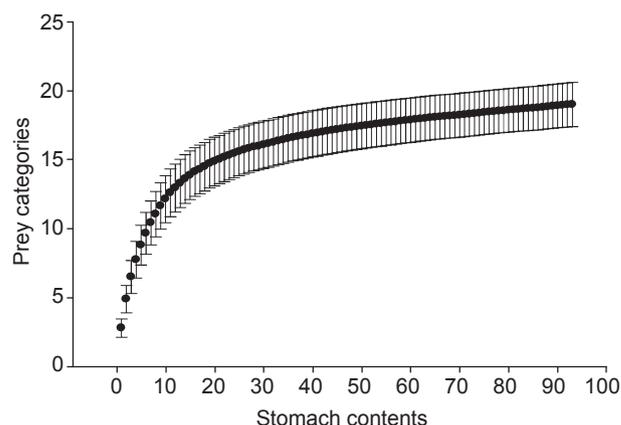


Fig. 1. Accumulation curve of prey categories consumed by *C. schmidti* in Turvo State Park, Rio Grande do Sul, Brazil ($n = 93$ stomach contents). Dots represent the mean, and bars represent the standard deviation from the mean.

Table 1. Prey categories consumed by *C. schmidti* in Turvo State Park, Rio Grande do Sul, Brazil ($n = 93$ stomach contents). F, total frequency; %F, relative frequency; N, total abundance; %N, relative abundance; V, total volume (mm^3); %V, relative volume; I_x , importance index

Prey category	F	%F	N	%N	V	%V	I_x
Insecta							
Formicidae	57	61.3	187	30.2	3471.6	20.4	37.29
Coleoptera	33	35.5	81	13.1	1661.65	9.7	19.44
Diptera	19	20.4	114	18.4	834.55	4.9	14.58
Coleoptera (larvae)	19	20.4	33	5.3	966.54	5.7	10.48
Diptera (larvae)	17	18.3	37	6	393.88	2.3	8.86
Collembola	18	19.4	26	4.2	215.75	1.3	8.27
Lepidoptera (larvae)	12	12.9	15	2.4	1280.23	7.5	7.61
Hymenoptera (not Formicidae)	15	16.1	15	2.4	53.05	0.3	6.29
Homoptera	13	14.0	16	2.6	153.53	0.9	5.82
Hemiptera	7	7.5	7	1.1	177.26	1.0	3.23
Blattaria	4	4.3	4	0.6	275.67	1.6	2.19
Psocoptera	5	5.4	5	0.8	44.54	0.3	2.15
Orthoptera	4	4.3	4	0.6	79.95	0.5	1.81
Lepidoptera	1	1.1	1	0.2	26	0.2	0.46
Trichoptera	1	1.1	1	0.2	2.91	0.0	0.42
Arachnida							
Araneae	19	20.4	35	5.7	608.56	3.6	9.88
Acari	4	4.3	5	0.8	4.81	0.0	1.71
Pseudoscorpiones	1	1.1	1	0.2	0.55	0.0	0.41
Mollusca							
Gastropoda	16	17.2	32	5.2	386.26	2.3	8.21
Artificial categories							
Unidentified arthropod remains	-	-	-	-	6330.27	37.1	-
Plant remains	-	-	-	-	85.48	0.5	-
Total			619		17,053		

Diptera (larvae) also had high importance values (Table 1). There was little difference in the most important prey categories for individual stomach contents (Fig. 2). The mean number of items found in stomachs was 6.66 (\pm 9.16), and the mean number of prey categories found was 2.85 (\pm 1.96).

The highest electivity was found for Gastropoda (D = 0.989), followed by Coleoptera (larvae) (D = 0.839) and Diptera (larvae) (D = 0.801), while the lowest values were obtained for Collembola (D = -0.892), followed by Orthoptera (D = -0.721) and Lepidoptera (D = -0.485). Prey items such as Diptera (D = 0.024), Formicidae (D = 0.214), and Araneae (D = 0.276) were consumed in proportions similar to those found in the environment. For prey items such as Psocoptera, Trichoptera, and Pseudoscorpiones, electivity was not calculated because they were not captured in pitfall traps (Table 2).

There were significant differences in the

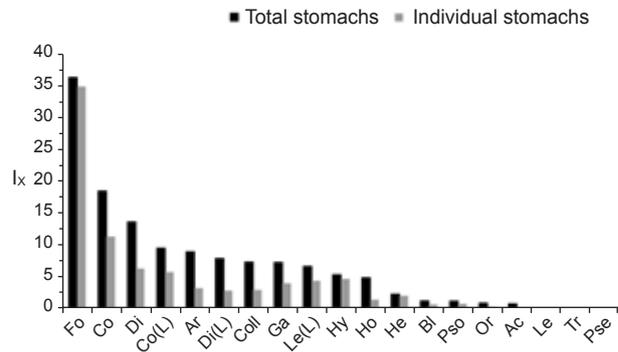


Fig. 2. Importance indices (I_x) for prey categories based on total and individual stomach contents of *C. schmidtii* in Turvo State Park, Rio Grande do Sul, Brazil. Ac, Acari; Ar, Araneae; Bl, Blattaria; Co, Coleoptera; Co(L), Coleoptera (larvae); Coll, Collembola; Di, Diptera; Di(L), Diptera (larvae); Fo, Formicidae; Ga, Gastropoda; He, Hemiptera; Ho, Homoptera; Hy, Hymenoptera (not Formicidae); Le, Lepidoptera; Le(L), Lepidoptera (larvae); Or, Orthoptera; Pse, Pseudoscorpiones; Pso, Psocoptera; Tr, Trichoptera.

Table 2. Electivity values of prey categories consumed by *C. schmidtii* in Turvo State Park, Rio Grande do Sul, Brazil ($n = 93$ stomach contents). N, total abundance; %N, relative abundance

Prey category	Diet		Environment		Electivity (D)
	N	%N	N	%N	
Insecta					
Coleoptera (larvae)	33	5.33	17	0.47	0.839
Diptera (larvae)	37	5.98	24	0.66	0.801
Blattaria	4	0.65	3	0.08	0.774
Homoptera	16	2.58	12	0.33	0.774
Hemiptera	7	1.13	7	0.19	0.710
Lepidoptera (larvae)	15	2.42	16	0.44	0.693
Coleoptera	81	13.09	159	4.36	0.489
Hymenoptera (not Formicidae)	15	2.42	34	0.93	0.444
Formicidae	187	30.21	580	15.91	0.214
Diptera	114	18.42	570	15.64	0.024
Lepidoptera	1	0.16	17	0.47	-0.485
Orthoptera	4	0.65	145	3.98	-0.721
Collembola	26	4.20	1872	51.36	-0.892
Plecoptera	0	0.00	1	0.03	-1.000
Psocoptera	5	0.81	0	0.00	-
Trichoptera	1	0.16	0	0.00	-
Arachnida					
Acari	5	0.81	11	0.30	0.456
Araneae	35	5.65	116	3.18	0.276
Opiliones	0	0.00	49	1.34	-1.000
Pseudoscorpiones	1	0.16	0	0.00	-
Mollusca					
Gastropoda	32	5.17	1	0.03	0.989
Crustacea					
Isopoda	0	0.00	1	0.03	-1.000
Other preys					
Oligochaeta	0	0.00	2	0.05	-1.000
Diplopoda	0	0.00	5	0.14	-1.000
Chilopoda	0	0.00	2	0.05	-1.000
Diplura	0	0.00	1	0.03	-1.000
Total	619	100	3645	100	

diet compositions between males and females ($G = 39.5$, $d.f. = 18$, $p = 0.002$) and between adults and juveniles ($G = 33.84$, $d.f. = 18$, $p = 0.01$) (Table 3). There were also significant differences with respect to the 3 most important items of each group between males and females ($G = 16.1$, $d.f. = 3$, $p = 0.001$) and between adults and juveniles ($G = 10.0$, $d.f. = 4$, $p = 0.04$).

The trophic spectrum of males consisted of 18 prey categories, the most important of which were Formicidae, Coleoptera, and Araneae, while the trophic spectrum of females comprised 15 categories, with Formicidae, Diptera, and Coleoptera being the most important prey categories. The juvenile diet included a lower trophic spectrum (13 categories) than that of adults (19 categories). Despite differences in diets between the sex and age groups, Formicidae represented the most important prey category for all of them (Fig. 3).

Even with a varied diet, *C. schmidti* presented a narrow niche breadth in terms of prey category consumption for the species and for the sex and age groups ($B_A < 0.5$), with low equitability in prey categories consumption. Furthermore, despite significant differences in diet compositions between males and females and between juveniles and adults, there was an overlap of 61% in the diet of males and females, and an overlap of 77% in the diet of adults and juveniles (Table 3).

No relationship was found for the mean length and volume of prey with the MW of individuals (prey mean length: $R^2 = 0.02$, $F_{1,76} = 2.37$, $p = 0.1$; prey volume: $R^2 = 0.004$, $F_{1,76} = 1.31$, $p = 0.25$). Regressions only considered MW as the predictor variable, because there were strong positive correlations between the morphological measures (SVL and MW: $r = 0.85$, $p < 0.001$; SVL and body

mass: $r = 0.88$; $p < 0.001$; MW and body mass: $r = 0.78$, $p < 0.001$; Fig. 4).

The mean male SVL was 26.65 ± 1.31 (range, 24.28-29.85) mm ($n = 58$), mean MW was 8.7 ± 0.4 (range, 7.67-9.82) mm ($n = 58$), and mean body mass was 2.14 ± 0.38 (range, 1.3-3.15) g ($n = 58$). The mean female SVL was 30.21 ± 1.66 (range, 27.15-33.31) mm ($n = 36$), mean MW was 9.41 ± 0.58 (range, 8.08-11.14) mm ($n = 36$), and mean body mass was 2.97 ± 0.48 (range, 2.05-4.1) g

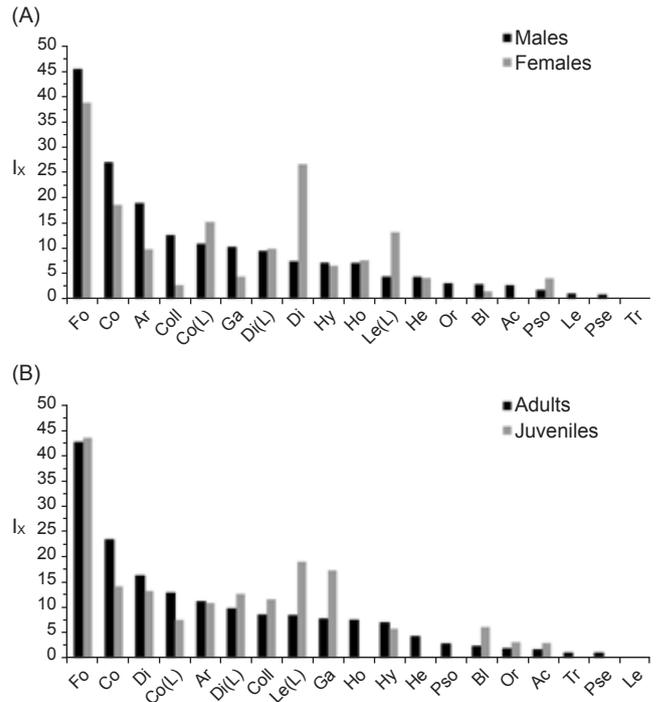


Fig. 3. Importance indices (I_x) for prey categories consumed by (A) males vs. females, and by (B) adults vs. juveniles of *C. schmidti* in Turvo State Park, Rio Grande do Sul, Brazil. Codes are explained in the legend to figure 2.

Table 3. Values of Levins' standardized niche breadth (B_A) for the species and sex and age groups, diet percentage overlap, and G test values regarding differences in diet between the sex and age groups of *C. schmidti* in Turvo State Park, Rio Grande do Sul, Brazil. *Indicates a statistically significant value by the G test

Group	Levins (B_A)	Percentage overlap	G test	p value
<i>C. schmidti</i>	0.295	-	-	-
Males	0.269	-	-	-
Females	0.271	-	-	-
Adults	0.292	-	-	-
Juveniles	0.399	-	-	-
Males vs. females	-	61%	39.55	0.002*
Adults vs. juveniles	-	77%	33.84	0.01*

($n = 36$). The mean juvenile SVL was 21.55 ± 1.6 (range, 19.04-23.91) mm ($n = 20$), mean MW was 7.12 ± 0.84 (range, 5.45-8.75) mm ($n = 20$), and mean body mass was 1.07 ± 0.23 (range, 0.75-1.5) g ($n = 20$).

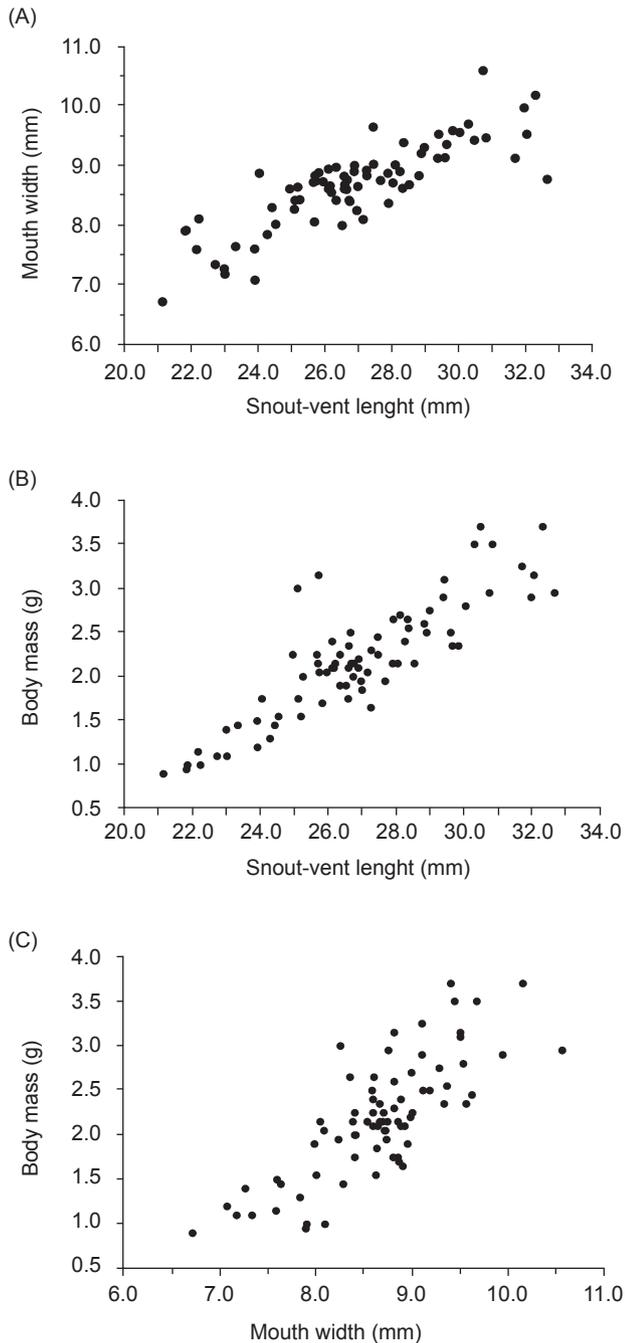


Fig. 4. Dispersion diagrams from Pearson's correlations between (A) snout-vent length and mouth width ($r = 0.85$, $p < 0.001$), (B) snout-vent length and body mass ($r = 0.88$; $p < 0.001$), and (C) mouth width and body mass ($r = 0.78$, $p < 0.001$) of *C. schmidtii* in Turvo State Park, Rio Grande do Sul, Brazil.

DISCUSSION

Crossodactylus schmidtii has the richest diet among hylodid species for which the diets are known. Despite differences in the number of stomach contents analyzed, studies have shown considerable similarity in diets of *Crossodactylus* and *Hylodes* species in terms of the most important prey items. The diet of *C. schmidtii* was primarily composed of insects, with ants, beetles, and dipterans being most important, which is similar to the diet of *C. aeneus* (Jordão-Nogueira et al. 2006). Similar results were found for *C. gaudichaudii* and *Hylodes fredii*, the former feeding mainly on ants, beetles, and insect larvae, and the latter mainly on insect larvae, beetles, and ants (Almeida-Gomes et al. 2007). Similarly, the most common prey in the diet of *C. bokermanni* are ants, dipterans, and insect larvae (Wachlevski et al. 2008), although the authors did not provide importance indices for prey categories.

Ants, the main item in the diet of *C. schmidtii*, are among the most abundant insects in the leaf litter and constitute the main prey consumed by many frogs (Toft 1980 1981, Donnelly 1991, Caldwell 1996, Darst et al. 2005). While some species have a diet composed exclusively of ants and termites, such as the microhylid *Elachistocleis bicolor* (Solé et al. 2002), other species can have a quite-varied diet despite the importance of ants in its composition. Species such as *Anomaloglossus stepheni* (Lima and Moreira 1993), *Ameerega flavopicta* (Biavati et al. 2004), *Thoropa miliaris* (Siqueira et al. 2006), and *T. taophora* (Brasileiro et al. 2010); for example, consume ants in large amounts but have varied diets. Studies on hylodid species also showed that their diets are composed of several prey categories, but with concentrated consumption of ants (Almeida-Gomes et al. 2007, Jordão-Nogueira et al. 2006, Wachlevski et al. 2008, this study).

Some items of major importance in the *C. schmidtii* diet (i.e., ants and dipterans) were related to their availability in the environment. According to Duellman and Trueb (1994), frogs can be considered opportunistic predators when the diet has some relationship with prey availability in the environment. On the other hand, *C. schmidtii* consumed low proportions of springtails and orthopterans despite their abundance in the environment. Springtails likely had a low electivity because they were much more abundant than other prey, constituting more than 50% of total available prey. Nevertheless, they were the 4th

prey category in importance in the male diet. Such small prey, as well as mites, are known to be important prey in the diet of small-sized frogs (Simon and Toft 1991, Lima and Moreira 1993).

The low proportion of gastropods and dipteran larvae in the environment resulted in high electivities, but it is possible that our prey sampling on the stream banks may have underestimated the availability of gastropods and dipteran larvae, which are usually found more frequently in water. Methods of assessing prey availability that do not cover all available microhabitats result in some electivity values that must be interpreted with care. Flowers and Graves (1995) studied the diets of 2 bufonids in North America and also found a bias in prey sampling in the environment, which underestimated the availability of insect larvae.

Ontogenetic changes in frogs' diets mainly occur due to morphological constraints, with individuals progressively consuming larger prey as they grow (Hirai 2002, Hirai and Matsui 2002). This relationship was observed for *C. aeneus* (Jordão-Nogueira et al. 2006), but not for *C. bokermanni* (Wachlevski et al. 2008), *C. gaudichaudii*, *Hylodes fredei* (Almeida-Gomes et al. 2007), or *C. schmidti* in the present study. Wachlevski et al. (2008) argued that the existence of a significant relationship may depend on the size range of the available prey, and on the level of species selectivity. The high consumption of small items like ants may reduce the variation in prey size in the diet, contributing to a lack of significance in relationships between prey size and predator size (Almeida-Gomes et al. 2007). Our results for *C. schmidti* of a lack of a significant correlation between prey and predator sizes are consistent with arguments of Wachlevski et al. (2008) and Almeida-Gomes et al. (2007).

Differences in diet compositions between males and females and between adults and juveniles of *C. schmidti* were significant. Between adults and juveniles, the difference may be related to a possible variation in foraging sites. Juveniles had a smaller trophic spectrum and consumed more gastropods than adults, suggesting a foraging behavior nearer the water, whereas adults had a larger trophic spectrum, suggesting that in addition to foraging in the water, they include terrestrial prey in their diet by foraging on the ground. In another study also conducted in Turvo State Park, adults of *C. schmidti* were found in pitfall traps installed hundreds of meters away from streams (Iop, pers. comm.), reinforcing our hypothesis that adults have higher mobility than juveniles, and are able to feed in sites that juveniles cannot reach.

Dietary differences between males and females of *C. schmidti* are more difficult to explain, since both sexes have the ability to forage at the same sites and eat the same prey. In *T. taophora*, a sexual difference in diet was assigned to foraging strategies; males are territorial sit-and-wait foragers and females are active foragers (Brasileiro et al. 2010). The territorial behavior of *C. schmidti* does not seem to limit their foraging areas; however, males can spend much time emitting aggressive calls during agonistic interactions with each other (Caldart et al. 2011). This suggests that dietary differences between males and females may be related to behavioral differences. Since females do not defend calling sites and do not spend time in agonistic interactions, it is likely that they can feed more frequently than males. The same was suggested for females of *Oophaga pumilio* (Donnelly 1991) and *Ranitomeya virolinensis* (Valderrama-Vernaza et al. 2009).

Even with a varied diet, *C. schmidti* presented a narrow niche breadth in terms of the consumption of prey categories, with a few categories comprising most of the diet (i.e., ants, beetles, and dipterans). The same tendency was observed when the niche breadth was separately analyzed for the different sex and age groups. The percentage overlap in the diets of adults and juveniles was higher (77%) compared to that of males and females (61%). Our estimation of prey availability suggests that food resources for *C. schmidti* were abundant in the streams studied, allowing the coexistence of both adults and juveniles, and males and females, despite their high dietary overlap. The considerable overlap in the diets of males and females of *T. taophora* (Brasileiro et al. 2010) was also interpreted as an indication of high prey availability, although the authors did not evaluate prey availability. Alternatively, segregation in time or in foraging sites could also allow for overlap in diets found for the sex and age groups of *C. schmidti*.

Considering its varied diet and relationships between some of the most important diet items and their availability in the environment, *C. schmidti* can be characterized as an opportunistic feeder with feeding habits similar to those of other *Crossodactylus* species, especially in the consumption of the most important prey such as ants, beetles, and dipterans. Toft (1981) observed a relationship between the degree of specialization in ants and the foraging strategy of diurnal litter frogs in Panama, where the diets of active-foraging species had high proportions of ants,

and the diets of sit-and-wait species rarely had ants. *Crossodactylus schmidti* can visually detect its prey at a few meters when foraging, and must have some plasticity in relation to the foraging strategy used, as it consumed both highly mobile (i.e. ants and dipterans) and less-mobile (i.e., insect larvae and gastropods) prey. Moreover, the fact that *C. schmidti* inhabits streams favors the consumption of both aquatic and terrestrial prey, contributing to a varied diet.

Similarities in the importance of prey such as ants, beetles, dipterans, and insect larvae in the diet of *Crossodactylus* species can be attributed to phylogeny and/or prey availability, as previously discussed by Wachlevski et al. (2008). Due to their phylogenetic proximity, it is expected that these similarities can also be found in other species of the genus *Hylodes*, as observed for *H. fredii* (Almeida-Gomes et al. 2007). However, it is difficult to assess the effects of phylogeny on the diet based on studies that do not evaluate prey availability. Dietary studies of other species are still needed to determine whether the high consumption of ants and similarities in the most important items are indicative of a pattern in diets of *Crossodactylus* and *Hylodes* species. We also highlight the importance of dietary studies that include prey availability, in order to better interpret the degree to which similarities in the diets are due to historical factors and/or to prey availability in the environment.

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