

FEEDING ECOLOGY OF *THOROPA TAOPHORA* (ANURA: CYCLORAMPHIDAE) ON A ROCKY SEASHORE IN SOUTHEASTERN BRAZIL

CINTHIA A. BRASILEIRO^{1,4}, MARCIO MARTINS² AND IVAN SAZIMA³

¹ Departamento de Ciências Biológicas, Universidade Federal de São Paulo, Rua Professor Artur Riedel, 275, 09972-270, Diadema, São Paulo, Brasil. cinthia_brasileiro@yahoo.com.br

² Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, 05508-900, São Paulo, Brasil.

³ Museu de Zoologia, Caixa Postal 6.109, Universidade Estadual de Campinas, 13083-970, Campinas, São Paulo, Brasil (retired and associated as researcher).

⁴ Corresponding author.

ABSTRACT. The rock frog (*Thoropa taophora*) dwells from rocky seashores to rocky outcrops within the Atlantic rainforest on coastal areas of the state of São Paulo, southeastern Brazil. In this study, we provide data on the food habits of a rock frog population focusing on ontogenetic, sexual, and seasonal variation. The study was based on the examination of 356 individuals (154 adults, 82 juveniles and 120 froglets). A total of 26 invertebrate types were found in the diet of *T. taophora*. The commonest prey types in the three size classes (adults, juveniles and froglets) of rock frogs were ants, both in frequency and number. Prey composition differed significantly among size classes, except for beetles and spiders. Prey composition of males and females also differed significantly: females had a high proportion of marine isopods, caddisfly nymphs, and orthopterans in the diet, whereas males had a high proportion of ants and caterpillars. Seasonal changes in diet (all significant) in the three size classes include froglets eating more springtails and less mites in the dry season, juveniles eating more marine isopods during the wet season (similar difference for adult males), and adult females eating more ants during the wet season.

KEYWORDS. rock frog; diet composition; ontogenetic variation; seasonal variation; Atlantic rainforest; South America.

INTRODUCTION

Thoropa taophora is a large cycloramphid frog that dwells from rocky seashores to rocky outcrops within the Atlantic rainforest (Bokermann, 1965; Sazima, 1971; Giaretta and Facure, 2004, all as *T. miliaris*) on coastal areas of the state of São Paulo, southeastern Brazil (Feio, 2004). Despite being a common and conspicuous species, surprisingly few studies deal with its natural history. The eggs are placed on rocks with dripping water, and the tadpoles develop at the same places after hatching (e.g., Siqueira *et al.*, 2006, as *T. miliaris*). Males are territorial and display parental care (Giaretta and Facure, 2004). The species's diet has been described based on short-term studies, which indicate that it feeds mostly on ants (Bokermann, 1965) and that individuals from populations dwelling close to the sea are able to prey on marine invertebrates (Sazima, 1971).

Herein, we provide data on the food habits of a *Thoropa taophora* population that dwells on a rocky seashore, sampled monthly throughout one year. We focused on four main questions: (1) what is the diet composition of the rock frog at a seashore site? (2) Are there ontogenetic changes in the diet, and of which type? (3) Are there sexual differences in the diet? (4) Is there any seasonal variation in the diet? We hypothesized that males, females, and juveniles would differ in their feeding ecology due to

differences in body size and behaviour, and that there would be seasonal variation in the diet of these three classes, due to differences in prey availability among seasons. Additionally, we hypothesized that marine prey would occur mostly in the diet of adults, given that they usually get closer to the sea compared to juveniles and froglets.

MATERIALS AND METHODS

The study was conducted at the Praia Domingas Dias (23°29'42"S; 45°08'52"W), municipality of Ubatuba, São Paulo State, southeastern Brazil. In this area, wet season lasts six months (October-March) and dry season equally lasts six months (April-September, see Hartman, 2004). The studied stretch of the rocky shore (Figure 1) extended from the forest edge to the low tide limit, comprising an area of about 650 m². The stretch was searched for 60 to 120 min two hours after nightfall, and 19 to 63 individuals were captured monthly from June 1971 to May 1972, totalling 356 specimens. All individuals were euthanized, immediately fixed in 10% formalin and stored in 70% ethanol, now in the Amphibian Collection of the Museu de Zoologia "Prof. Adão José Cardoso" at the Universidade Estadual de Campinas (ZUEC), São Paulo, Brazil. Snout-urostyle length (SUL) and jaw width (JW) of all specimens were measured with

callipers to the nearest 0.01 mm. Frogs were grouped into three broad size classes: froglets (10-30 mm), juveniles (31-50 mm), and adults (51-92 mm). Froglets and juveniles had undetermined sex, whereas adults were males (thickened forelimbs and small spines on fingers) and females (slender forelimbs with no spines, and discernible ovaries) (Feio, 2004). Stomachs were removed through an abdominal incision and preserved in 70% ethanol, their contents being analyzed qualitatively and quantitatively. Today other methods to study diet are used, such as stomach-flushing, but these methods were not well established at the time the frogs analyzed here were collected.

Prey were identified under a stereomicroscope to order (or family for ants), and quantified and measured (total length) with calliper or under a stereomicroscope. Prey were grouped into four length classes: diminutive (0.1-2.0 mm), very small (2.1-5.0 mm), small (5.1-10 mm), and large (> 10 mm).

To examine diet composition, we considered the frequency of occurrence of each prey category (number of stomachs that contained a given category), and the numeric proportion of each prey category (number of individuals of each prey category divided by the total number of consumed preys). Most prey categories were poorly represented in the diet of all size classes (Table 1). Thus, for the analyses of sexual and ontogenetic variation we excluded prey that represented less than 3% of analyzed stomachs. To compare differences in diet composition (based on numeric proportions of prey categories) between sexes, size classes, and seasons we used G-tests. We

examined differences between size classes using Pianka's measure of niche overlap (Pianka, 1973). We compared the observed overlap value against a null model (1000 iterations) generated by the algorithm of randomization RA3 (Lawlor, 1980), using the software ECOSIM 7.0 (Gotelli and Entsminger, 2001). In addition, the niche breadth was calculated for numerical data using the following formula (Simpson, 1949): $B = 1/\sum p_i^2$, where p is the proportion of prey category i in the diet. These analyses were used to examine sexual and seasonal differences as well. Differences in SUL between sexes were tested with an one-way analysis of variance (ANOVA); to test for differences in jaw width between sexes we used an analysis of covariance (ANCOVA; with SUL as covariate). To investigate the effect of body size on prey size (jaw width and SUL of the frog on largest prey per stomach) and prey consumption (SUL of the frogs on the number of prey in the stomach), we used a Simple Regression Analysis (variables were log-transformed; Zar, 1999). G-tests and regressions were performed with the software BioStat, and ANOVAs and ANCOVAs were performed with Statistica. Significance was assessed based on $\alpha = 0.05$.

RESULTS

Adults of both sexes wandered into the intertidal zone of the rocky shore during low tides (Figure 2). Only 3% of 356 individuals (154 adults, 82 juveniles and 120 froglets) had empty stomachs. A total of 26



FIGURE 1. Rocky seashore at the Praia Domingas Dias, Ubatuba, São Paulo, southeastern Brazil, habitat of the rock frog *Thoropa taophora*. The two yellow vertical lines delimit the studied stretch.

TABLE 1. Prey types of a rocky seashore population of *Thoropa taophora* (Anura, Cycloramphidae) in Ubatuba, São Paulo, southeastern Brazil. Number (Np) and frequency (F) of each prey category. (L) = Larvae. N = number of stomachs.

	Adults (N = 154)		Juveniles (N = 82)		Froglets (N = 120)	
	Np (%)	F (%)	Np (%)	F (%)	Np (%)	F (%)
Gastropoda	2.0	0.9	—	—	—	—
Arachnida						
Araneida	19.6	2.4	4.1	10.9	2.4	5.4
Scorpionida	—	—	0.1	0.4	—	—
Acarina	—	—	—	—	7.9	5.4
Miriapoda						
Diplopoda	2.6	0.3	0.1	0.4	—	—
Chilopoda	2.0	0.3	—	—	0.1	0.3
Crustacea						
Isopoda	35.9	13.1	16.8	10.1	1.6	4.4
Other	7.9	1.1	0.2	0.8	0.4	1.6
Insecta						
Collembola	1.3	0.5	0.3	1.3	25.5	7.9
Orthoptera	27.4	3.1	2.0	5.5	0.9	1.6
Odonata	—	—	0.1	0.4	—	—
Hemiptera	6.5	0.8	1.1	3.4	1.7	5.1
Homoptera	2.6	0.3	0.7	2.5	0.3	1.3
Coleoptera	36.6	5.1	6.7	13.9	3.9	11.4
Coleoptera (L)	3.3	0.3	0.6	2.1	0.5	1.9
Hymenoptera						
Formicidae	71.2	63.8	60.0	29.8	37.5	24.9
Other	3.2	1.2	0.2	0.8	0.4	1.6
Trichoptera (L)	13.7	2.4	0.5	1.3	2.9	2.5
Psocoptera	2.61	0.6	0.1	0.4	—	—
Thysanoptera	—	—	—	—	0.1	0.3
Dermaptera	—	—	—	—	0.1	0.3
Lepidoptera (L)	7.2	4.2	—	—	0.6	1.6
Diptera	4.6	1.8	2.7	7.1	5.0	10.8
Diptera (L)	3.3	1.8	0.7	2.5	8.4	12.7
Arthropod remains		4.2	0.2	0.8	0.1	0.3
Plant remains		3.6	0.3	1.3	—	—
<i>T. taophora</i> eggs	0.6	3.6	—	—	—	—
<i>T. taophora</i> larvae	0.6	1.2	—	—	0.1	0.3

invertebrate types were found in the diet of *T. taophora* (considering all size classes, Table 1). The mean number of preys per stomach was 10.3 ± 14.9 (N = 1493; range: 1-107) for adults, 10.8 ± 10.4 (N = 1393; range: 1-50) for juveniles, and 11.6 ± 15.4 (N = 845; range: 1-120) for froglets. The commonest prey types for the three size-classes of frogs were ants, both in frequency and number (Figure 3). Except for the froglets, the second and third most important preys in frequency were marine isopods (*Ligia exotica*) and beetles (Figure 3). Another marine prey was

the crab *Pachygrapsus transversus*, found in the diet of all three size-classes (see Crustacea – other, in Table 1). Springtails (Collembola) and mites (Acarina) were important in the diet of froglets only (Figure 2). Most prey were invertebrates, exceptions being conspecific eggs and tadpoles, found in low frequency in the diet of males (N = 7) and froglets (N = 1).

Prey composition of adults, juveniles, and froglets differed significantly ($G = 1274$; $P < 0.01$; Figure 3), except for beetles ($P = 0.1$) and spiders ($P = 0.9$) (Figure 2). The diet of adults was more similar to that of juveniles ($G = 153.1$; $P < 0.01$) than to that of froglets ($G = 876.6$; $P < 0.01$). The diet of juveniles was composed of subsets of that of adults with a few components of that of froglets ($G = 709.2$; $P < 0.01$).



FIGURE 2. An adult male rock frog (*Thoropa taophora*) foraging at low tide in the dry season on rocky seashore at the Praia Domingas Dias, Ubatuba, São Paulo, southeastern Brazil. Note mussels (black), barnacles (white), and seaweeds (green).

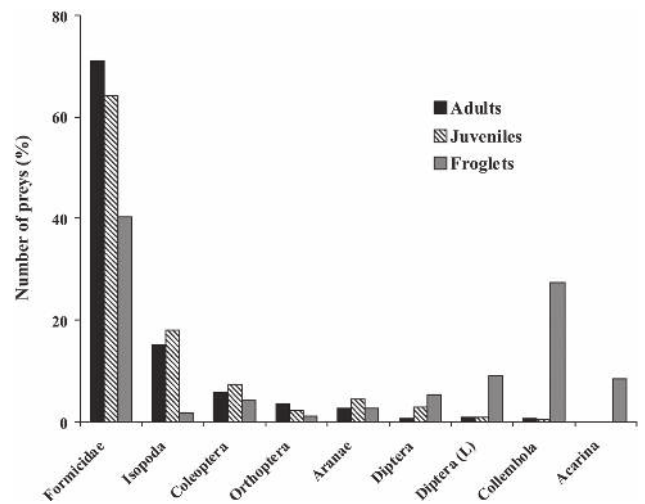


FIGURE 3. Number of preys (%) of the most important prey categories for each size class of *Thoropa taophora* on a rocky seashore, Ubatuba, southeastern Brazil. L = larvae.

TABLE 2. Mean and standard deviation of SUL (snout-urostyle length, mm) and jaw width of *Thoropa taophora* from Ubatuba, São Paulo, southeastern Brazil.

Categories	N	SUL	JW
Males	70	70.3 ± 10.4 (55-93)	28.3 ± 4.6 (21.4-38.6)
Females	85	61.8 ± 4.84 (51-74.5)	23.3 ± 2.4 (18.9-33.0)
Juveniles	78	39.5 ± 5.5 (31-52)	14.3 ± 2.8 (10.7-24.6)
Froglets	117	20.7 ± 5.8 (10-29.95)	7.4 ± 2.1 (3.4-13.3)

Although ants made up a large portion of the diet of all three size-classes, they were more important in the diet of adults than in those of the other two size-classes (Figure 3). Froglets had a diverse array of prey types in their diets and, with the exception of ants, the commonest preys were springtails and flies (adults and larvae). Mites were consumed by froglets only (Figure 3).

Adults and juveniles had a substantial niche overlap for the most important preys (Figure 3; $O_{jk} = 0.99$, $P < 0.01$), whereas froglets had a low niche overlap with both adults and juveniles (adults: $O_{jk} = 0.79$; juveniles: $O_{jk} = 0.78$; $P = 0.94$). The trophic niche of adults ($B = 2.05$) was narrower than those of juveniles ($B = 2.20$) and froglets ($B = 3.86$) regarding prey types. Prey size showed little overlap among frog size classes, and varied from 0.2 to 19 mm ($\bar{X} = 2.9 \pm 2.4$; $N = 101$) for froglets; 1.2 to 19 mm ($\bar{X} = 5.0 \pm 2.7$; $N = 80$) for juveniles, and 1.9 to 30 mm ($\bar{X} = 9.1 \pm 4.6$; $N = 145$) for adults. In general, adults consumed large

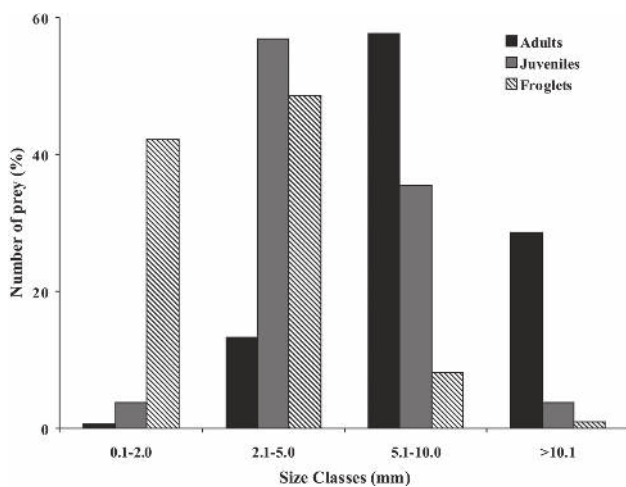


FIGURE 4. Prey size (mm) eaten by adults, juveniles and froglets of *Thoropa taophora* on a rocky seashore in Ubatuba, southeastern Brazil.

preys whereas froglets ate small ones (Figure 4). We found a relatively strong effect of frog jaw width on maximum prey size ($F = 316$; $R^2 = 0.54$; slope = 0.57; $P < 0.001$), as well as of snout-urostyle length on maximum prey size ($F = 396.6$; $R^2 = 0.56$; slope = 0.57; $P < 0.001$). We also found a weak effect of snout-urostyle length on the number of preys in the stomach ($F = 4.58$; $R^2 = 0.15$; slope = -0.076; $P < 0.05$).

Males were significantly larger than females ($t = 6.2$, $P < 0.01$, Table 2) but there was no sexual difference in jaw width ($F_{1,102} = 1.42$, $P = 0.23$; Table 2). The mean number of preys per stomach was 8.6 ± 13.5 ($N = 70$; range: 1-80) for males and 10.9 ± 15.6 ($N = 82$; range: 1-102) for females. Prey size was 2.4-20 mm ($\bar{X} = 8.6 \pm 3.6$; $N = 876$) for males, and 1.9-30 mm ($\bar{X} = 9.7 \pm 5.6$; $N = 607$) for females. Diet composition of males and females differed significantly ($G = 86.0$, $P < 0.001$). Females had a higher proportion of marine isopods (G -test = 22.9; $P < 0.01$; Figure 5), larval caddisflies (Trichoptera) (G -test = 15.7; $P < 0.001$), and orthopterans (G -test = 10.96; $P < 0.01$) in the diet, whereas males had a higher proportion of ants (G -test = 15.7; $P < 0.01$) and caterpillars (G -test = 11.5; $P < 0.001$; Figure 5). Males and females showed a substantial niche overlap across the most important prey categories ($O_{jk} = 0.997$, $P < 0.01$; Figure 5). The trophic niche of males ($B = 1.7$) was slightly narrower than that of females ($B = 2.0$).

Seasonal changes in diet composition were evident in all size classes (Figure 6). Niche overlap was high between adults and juveniles in the wet season ($O_{jk} = 0.98$; $P < 0.01$). However, the trophic overlap

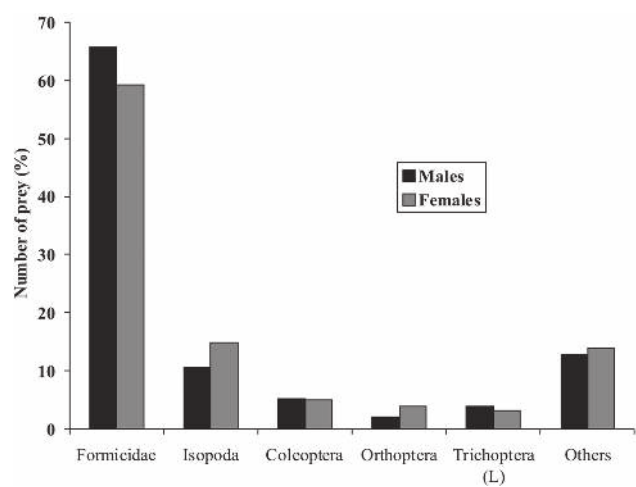


FIGURE 5. Number of preys (%) in the diet of males and females of *Thoropa taophora* on a rocky seashore, Ubatuba, southeastern Brazil. L = larvae.

was not significant between froglets and juveniles, and between froglets and adults (adults-froglets: $O_{jk} = 0.76$; juveniles-froglets $O_{jk} = 0.74$; $P = 0.9$). Froglets ate a higher number of fly larvae, springtails and mites (Figure 6), which were rare in the diet of larger individuals. Trophic overlap between adults and juveniles was also very high during the dry season ($O_{jk} = 0.99$; $P < 0.01$). Niche overlap between adults and froglets ($O_{jk} = 0.79$; $P = 0.9$) was a little higher in the dry season than in the wet season, although such overlap was not significant. Niche overlap between the diet of juveniles and froglets ($O_{jk} = 0.81$; $P < 0.01$) was higher in the dry season than in the wet season. Comparing wet and dry seasons, there were significant differences in the proportion of some of the six most important preys of froglets (G-test = 28.9; $P < 0.01$), but such differences were not detected for adults (G-test = 3.46; $P > 0.05$) nor juveniles (G-test = 10.8; $P > 0.05$). In the dry season, froglets ate significantly more springtails (G-test = 20.5; $P < 0.01$) and less mites (G-test = 5.5; $P < 0.01$) than in the wet season (Figure 6). Juveniles ate significantly more marine

isopods during the wet season (G-test = 9.8; $P < 0.01$; Figure 6). Males ate significantly more marine isopods during the wet season (G-test = 3.7; $P < 0.05$), whereas females consumed more ants during the wet season (G-test = 6.9; $P < 0.01$). There were no significant differences between the two seasons for other prey types (Figure 6).

DISCUSSION

Thoropa taophora is a trophic generalist like its congener *T. miliaris* (Siqueira *et al.*, 2005) and some other Atlantic forest frog species (Sabagh and Carvalho-e-Silva, 2008; Almeida-Gomes *et al.*, 2007; Marra *et al.*, 2004; Van Sluys *et al.*, 2001). Diet composition of *Thoropa taophora* was slightly more diverse (25 taxa) than that of other frog species from the Atlantic forest (*Crossodactylus aeneus*, 17 taxa; *Ischnocnema parva*, 17 taxa; Jordão-Nogueira *et al.* 2006), including other cycloramphid frogs (*Zachaenus parvulus*, 22 taxa; *Proceratophrys appendiculata*, 8 taxa; *P. boiei*,

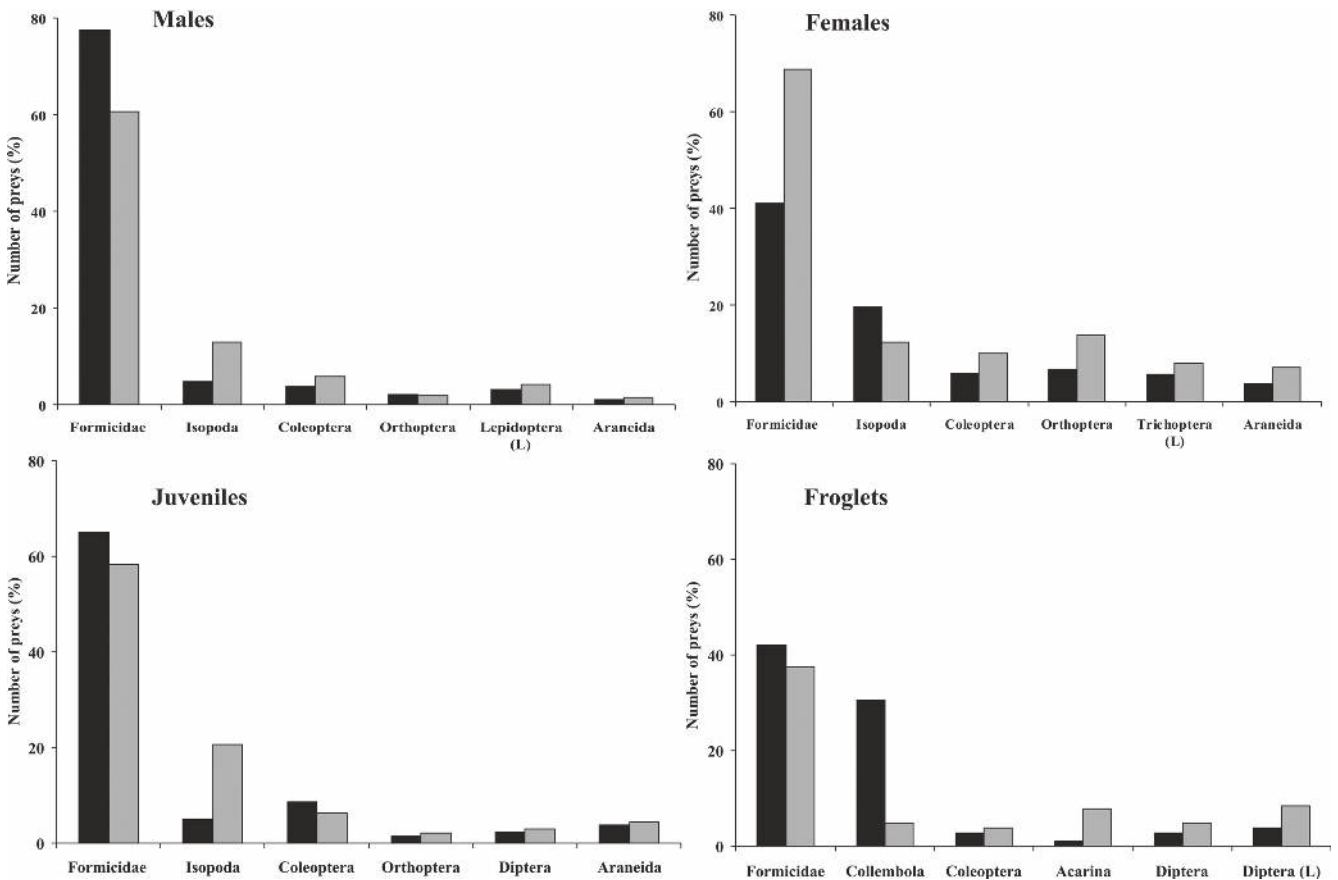


FIGURE 6. Seasonal variation in the diet of *Thoropa taophora* on a rocky seashore, in Ubatuba, southeastern Brazil: Black bars = dry season; gray bars = wet season; L = larvae.

23 taxa; Van Sluys *et al.*, 2001; Boquimpani-Freitas *et al.*, 2002; Giaretta *et al.*, 1998, respectively) and its congener *T. miliaris* (22 taxa; Siqueira *et al.*, 2005).

Regarding the number of preys, ants were the commonest items preyed (60%) by *T. taophora*, similar to what has been described for *T. miliaris* (Siqueira *et al.*, 2005) and other cycloramphid frogs from the Atlantic forest (Van Sluys *et al.* 2001; Almeida-Gomes *et al.*, 2007). Mites and springtails are known to be important components of the diet of very small frog species (e.g., Marra *et al.*, 2004; Juncá and Eterovick, 2007) and of recently-metamorphosed individuals and juveniles of larger species (e.g., Lima and Moreira, 1993; Lima and Magnusson, 1998). The low number of empty stomachs throughout the study indicates that there were optimal feeding conditions for frog survival at our study site, as suggested by Kovács *et al.* (2007) for the European hyloid frog *Hyla arborea*.

Adults, juveniles, and froglets occupied the same general habitat, and thus likely experienced the same prey availability. However, diet composition differed among frogs of different sizes (= ages), mainly between froglets and adults. Froglets consumed more small preys like mites and springtails, whereas adults consumed large preys like beetles and grasshoppers. In this case, selection for different prey sizes possibly resulted from morphological limitations such as gape. Important exceptions were ants, since all three frog size-classes consumed this prey type (curiously, the proportion of ant prey was much higher in adults than in either juveniles or froglets). This latter trend may be explained by the clumping behaviour of ants, and small catching effort for this prey once located. In spite of evident morphological limitation (body size, jaw width), ontogenetic changes in prey consumption may be due to differences in the electivity of prey type and/or related to the foraging mode. Juveniles and froglets had a tendency to move more than adults on the studied stretch. Adult males were more stationary, likely due to their territorial habit (Giaretta and Facure, 2004). Only 16% and 8% of the prey types were eaten exclusively by froglets/juveniles and adults, respectively. Thus, morphological constraints seem more important for prey selection than behaviour.

Males and females showed similar food niche breadth (both seasons pooled). However, females ate more marine isopods, trichopteran nymphs, and orthopterans, whereas males ate more ants. Differences in the diet of males and females could be explained by differences in foraging modes. Males are territorial (Giaretta and Facure, 2004), while females wander on the seashore (I. Sazima, pers. obs.), which strongly

indicates that males tend to be ‘sit-and-wait’ predators (especially at the reproductive peak, see below) and females tend to be active foragers. Thus, males and females mostly used different microhabitats, and consequently found different prey types (see Saenz, 1996). The substantial niche overlap indicates that there was high food availability and this likely allowed the coexistence of males and females with little or no competition (see Juncá and Eterovick, 2007). *Thoropa taophora* males can select larger preys to maximize energetic input during territory defence and brood care (see Giaretta and Facure, 2004). In contrast, some studies showed that females of other anuran species select larger preys compared to males, and suggested that the extra energy is invested in reproductive effort (Biaviati *et al.*, 2004; Juncá and Eterovick, 2007).

Seasonal diet composition was different for all groups analyzed. For instance, males ate more ants in the dry season, while females ate more ants in the wet season; females also ate more grasshoppers in the wet season, while males ate more marine isopods in this season. The wet season coincides with the peak of reproductive activity of this frog (Hartmann, 2004), which could explain, at least partly, these differences. Males tend to be stationary during the wet season due to their territoriality (Giaretta and Facure, 2004), as mentioned above, and wander more during the dry season (I. Sazima, pers. obs.). However, tides and surf generally are more extreme during the wet season than during the dry season at the study area, which would explain more marine preys in the diet of males (marine isopods tend to move upwards the shore during high tides and surf). The consumption of marine preys plus incursions to intertidal habitat (Sazima, 1971) and its osmotic consequences on *T. taophora* body are managed by means of its variable osmotic concentration (Abe and Bicudo, 1991). There were also evident seasonal changes in the diet composition of juveniles and froglets. Particularly, springtails were consumed by froglets much more frequently in the wet season, whereas mites were consumed more frequently in the dry season. Juveniles ate more isopods in the wet season (see above for more extreme tides). These seasonal differences in the diet likely are due to different use of habitat and/or behaviour in different periods of the year. During the dry season, froglets and juveniles tended to remain near the forest edge (I. Sazima, pers. obs.), a habitat wetter than the rocky shore. As weather conditions influence the dynamic of prey populations and frogs’ activities, both factors may influence diet composition. No detailed foraging or habitat use studies on *T. taophora* or their

congeners are available, and thus it is not possible to properly evaluate the importance of behaviour for seasonal differences of its diet. Availability of different prey throughout the year is another point in need of evaluation. Future studies on the rock frog in habitats close to seashore may focus on differences in microhabitat use by males, females, juveniles, and froglets, and their foraging modes in the two contrasting seasons (wet and dry), which would help to understand whether ontogenetic changes are due to differences in electivity of prey or due to prey size preferences and/or due to differences in size and gender.

RESUMO

O sapo-bode (*Thoropa taophora*) vive em costões rochosos e afloramentos rochosos na Mata Atlântica da costa do Estado de São Paulo, sudeste do Brasil. Neste estudo, apresentamos informações sobre os hábitos alimentares de uma população de sapo-bode, com ênfase nas variações ontogenéticas, sexuais e sazonais. O estudo foi baseado no exame de 356 indivíduos (154 adultos, 82 juvenis e 120 recém-metamorfoseados ou próximos a esse estágio). Um total de 26 tipos de invertebrados foi encontrado na dieta de *T. taophora*. As presas mais comuns nas três classes de tamanho dos anuros (adultos, juvenis e recém-metamorfoseados) foram formigas, tanto em frequência quanto em número. A composição da dieta diferiu significativamente entre as classes de tamanho, exceto para besouros e aranhas. A composição da dieta dos machos e fêmeas também diferiu significativamente. As fêmeas apresentaram maior proporção de isópodes marinhos, tricópteros (ninfas) e ortópteros, ao passo que os machos apresentaram maior proporção de formigas e larvas de lepidópteros. Alterações sazonais na composição da dieta (todas significativas) das três classes de tamanho incluem recém-metamorfoseados consumindo mais Collembola e menos Acari na época seca, juvenis consumindo mais Isopoda marinhos na época úmida (diferença semelhante para machos adultos), e fêmeas adultas consumindo mais Formicidae na época úmida.

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