Feeding overlap in two sympatric species of *Rhinella* (Anura: Bufonidae) of the Atlantic Rain Forest

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ABSTRACT. A clear understanding of the relationships between overlapping, similarity, and competition is necessary to understand many of the questions about the structure and operation of a community. *Rhinella icterica* (Spix, 1824) and *Rhinella crucifer* (Wied Neuwied, 1821) are sympatric species of toads occurring in the National Park of Serra dos Órgãos in southeastern Brazil. The aim of the present study was to assess the dietary overlap of these two species. Ninety-four stomachs were analyzed, and 2245 prey items were found. Common prey were Hymenoptera, Coleoptera, Diptera, Lepidoptera larvae, Blattaria, Orthoptera, Hemiptera, Opiliones, and Aranaea. Ants were the most important prey in both diets, followed by beetles and cockroaches. The niche breadth of *R. icterica* was 1.76 and of *R. crucifer* was 1.28. The dietary overlap between the species was 98.62%. A positive correlation was observed between jaw width and prey size consumed by *R. icterica*.
KEY WORDS. Amphibia; diet; *Rhinella crucifer*; *Rhinella icterica*.

RESUMO. **Sobreposição alimentar em duas espécies simpátricas de *Rhinella* (Anura: Bufonidae) da Mata Atlântica.** Um claro entendimento das relações entre sobreposição, similaridade e competição é necessário para entender muitas questões sobre a estrutura e o funcionamento de uma comunidade. *Rhinella icterica* (Spix, 1824) e *Rhinella crucifer* (Wied Neuwied, 1821) são espécies simpátricas que ocorrem no Parque Nacional da Serra dos Órgãos, região sudeste do Brasil. O objetivo do presente estudo foi verificar a sobreposição alimentar dessas duas espécies. Foram analisados 94 estômagos e encontradas 2245 presas. Os grupos comuns foram: Hymenoptera, Coleoptera, Diptera, larva de Lepidoptera, Blattaria, Orthoptera, Hemiptera, Opiliones e Aranaea. Formigas foram as presas mais importantes na dieta, seguidas por besouros e baratas. A amplitude de nicho de *R. icterica* foi de 1,76 e a de *R. cruicifer* 1,28. A sobreposição de nicho alimentar entre as espécies foi de 98,62%. Houve relação positiva entre a largura da mandíbula e a dimensão das presas consumidas em *R. icterica*.
PALAVRAS CHAVE. Amphibia; dieta; *Rhinella crucifer*; *Rhinella icterica*.

Resource partition in a community is essential for the understanding of species interactions. Species may be compared on the basis of morphology, microhabitat use, foraging time, and resources consumed (LAWOR 1980). Diets are a fundamental aspect of each niche, and it seems reasonable to assume that the structure of a community is based mostly on the way that food is shared among coexisting species (ANDREW & CHRISTENSEN 2001).

Many studies have been conducted on sympatric amphibians, on their feeding and dietary overlap (TOFT 1980, LIMA & MAGNUSSON 1998, VAN SLUYS & ROCHA 1998, DURÉ & KEHR 2001, 2004, ISACCH & BARG 2002, MENIN *et al.* 2005), microhabitat use (VAN SLUYS & ROCHA 1998, DURÉ & KEHR 2004, MENIN *et al.* 2005), and foraging time (LIMA & MAGNUSSON 1998, MENIN *et al.* 2005).

The Bufonidae is one of the most widely distributed anuran families in the world. According to an extensive systematic revision (FROST *et al.* 2006), many species of *Bufo* Laurenti, 1768 were allocated to the revalidated *Chaunus* Wagler, 1828. However, another study (CHAPARRO *et al.* 2007) recommended the generic name *Rhinella* Fitzinger, 1826, because *Rhinella* was found to be nested within *Chaunus*. *Rhinella icterica* (Spix, 1824) and *Rhinella crucifer* (Wied Neuwied, 1821) are sympatric species and share resources as well as call sites and reproduction habitats in the Serra dos Órgãos National Park. *Rhinella icterica* (*marinus* group) is distributed through southeastern Brazil, south to eastern Paraguay and the province of Misiones in Argentina. *Rhinella crucifer* (*crucifer* group) occurs from Misiones and the northeastern province of Corrientes in Argentina north to eastern Paraguay and southeastern, eastern, and northeastern Brazil (FROST 2007, MARQUES *et al.* 2006). Both species have similar reproductive habits and vocalizations (IZECKSOHN & CARVALHO-E-SILVA 2001). HADDAD *et al.* (1990) reported natural hybridization between both species, although the progeny are inviable, generating no descendents.

The aim of the present study was to assess the existence of feeding overlap between these two species of toads in the National Park of Serra dos Órgãos, state of Rio de Janeiro, Brazil.

MATERIAL AND METHODS

The National Park of Serra dos Órgãos (PARNA/SO) is located in southeastern Brazil, state of Rio de Janeiro, at 22º26' S, 42º59' W (altitude about 995 m). It is located in the biogeographical province of Serra do Mar and in the Tropical Atlantic morphoclimatic domain. It is situated in a climactic strip that varies from hot to super-hot and super-humid, with a general tropical super-humid climate (80 to 90% relative humidity), an annual mean temperature of 13 to 23ºC, and a mean annual precipitation of 1,700 to 3,600 mm (IBAMA 2007). The vegetation is a dense ombrophilous forest, which harbors a diverse anuran fauna.

Sampling was carried out from December 2004 to February 2007, non-periodically, totalling roughly 270-field hours. Anurans were collected manually. The snout-urostyle length (SUL) and jaw width (JW) were measured by means of a caliper to the nearest 0.1 mm. All measurements are presented in the following sequence: mean followed by maximum-minimum and standard deviation. A stomach-flushing method adapted from LECLERC & COURTOIS (1993) was used to collect food items. Anurans that had their stomachs flushed were marked with a color code to avoid pseudoreplication, and were returned to the area where they were found. The obtained items were measured as length and width (with a caliper to the nearest 0.1 mm) and their volume was estimated by the ellipsoid formula $V = 4/3.\pi.L/2.(W/2)2$ (Colli & Zamboni 1999), where L = item length and W = item width.

Snout-urostyle length and jaw width of both species were compared using Student's t test (Zar 1999), to assess morphological differences. An index of relative importance (IRI), proposed by PIANKA *et al.* (1971) was used, IRI = %O.(%N + %V) where %O = relative occurrence; %N = relative abundance and %V = relative volume. The trophic niche breadth was calculated using the formula proposed by LEVINS (1968) $B = 1/ \Sigma p_j^2$, where B = niche breadth and pj = proportion of item j in the diet. To restrict the breadth to a known interval from 0 to 1, the formula $B_A = B–1/n–1$ was used, where B_A = standardized Levins index and n = number of possible resources. An overlapping niche was used only when the species were collected simultaneously, to avoid influencing results via resource availability. The overlapping formula $C_H = 2\Sigma p_{ij}p_{ik}/\Sigma p_{ij}^2 + \Sigma p_{ik}^2$, was used, where CH = Morisita-Horn index (Horn 1966) of niche overlap, p_{ij} = corresponding proportion of resource i in the total resource used by species j, p_{ik} = corresponding proportion of resource i in the total resource used by species k. The index ranges from 0 to 1, where 0 indicates no overlapping and 1 indicates total overlapping. A simple linear regression was plotted between prey size (mean, highest and lowest volume per stomach) and jaw width, total volume per stomach versus SUL, and total number of prey items per stomach versus SUL.

RESULTS

Ninety-four stomachs were analyzed; 64 belonged to *R. icterica* (51 males, 13 females) and 30 to *R. crucife*r (28 males, 2 females). Four of the stomachs were empty (4.26%). The SUL (*R. icterica* 91.43; 62.8-155.0; 20.01) (*R. crucifer* 69.70; 58.1-90.2; 7.10) and JW (*R. icterica* 34.42; 22.0-58.7; 7.80) (*R. crucifer* 23.77; 18.6-30.5; 2.67) showed significant differences between the species ($p < 0.01$; $T_{SUL} = 5.768$ with 92 degrees of freedom; $T_{JW} = 7.297$ with 90 degrees of freedom).

We found 2,245 food items, which are listed in table I. All items that could be identified to different taxonomic levels are listed in table II. Traces of molted skin were recorded in three stomachs (two *R.icterica* and one *R. crucifer*) but were not quantified. Plant remains such as leaves, small twigs and seeds, as well as dirt and small stones were also observed in 44 (46.81%) stomachs (36 *R. icterica* and eight *R. crucifer*). Plastic from candy and cigarette packages, small styrofoam spheres, and strands of hair were found in some stomachs.

Rhinella icterica had 27 food items, whereas *R. crucifer* had only 16. Preys common to both species were: Hymenoptera, Coleoptera (adults and larvae), Diptera (adults and larvae), Lepidoptera larvae, Blattaria, Orthoptera, Hemiptera, Opiliones, and Araneae. Items consumed only by *R. icterica* were: adult Lepidoptera, adult Tricoptera, Neuroptera larvae, winged Isoptera, Dermaptera, Plecoptera and Odonata naiads, Ephemeroptera subimagos, Isopoda, Diplopoda, Chilopoda, Oligochaeta, and Gastropoda. Items consumed only by *R. crucifer* were: Colembolla, Hirudinea, and Nematomorpha.

Ants were the dominant prey, with the highest absolute values in all analyzed stomachs. Excluding empty stomachs, there was 100.0% ant occurrence in *R. icterica* and 90.0% in *R. crucifer*. Beetles were important in both diets, especially in *R. icterica,* where their relative volume was twice that of ants. However, according to the IRI (Tab. I), ants were the most important items in the diet of both species, particularly *R. crucifer*. Beetles were the second most important item in both diets, with occurrence and frequency inferior only to ants. In *R. icterica*, a larger relative volume of beetles was found (Tab. I).

Rhinella icterica niche breadth was $B = 1.76$ ($B_A = 0.03$), and that of *R. crucifer* was $B = 1.28$ ($B_A = 0.02$), and the feeding niche overlap between species was 98.62%. There was a significant positive correlation in all three *R. icterica* regressions ($p < 0.05$) (JW x Higher vol. $r^2 = 0.1741$; $p = 0.0091$; JW x Lower vol. $r^2 = 0.1006$; $p = 0.0135$; JW x Mean vol. $r^2 = 0.1428$; $p = 0.0029$). No regressions between JW of *R. crucifer* and prey size were significant ($p > 0.05$) (JW x Higher vol. $r^2 = 0.1094$ $p = 0.0798$; JW x Lower vol. $r^2 = 0.0096$ $p = 0.6133$; JW x Mean vol. $r^2 = 0.0853$ $p = 0.1241$).

The regression between total volume per stomach and SUL for *R. icterica* was significant ($r^2 = 0.1225$ $p = 0.01$). For *R. crucifer* this regression was not significant ($r^2 = 0.0064$ $p = 0.67$). No regressions between total number of prey items per stomach and SUL were significant ($p > 0.05$).

DISCUSSION

Although these toads differ in size, their diets were quite similar. *Rhinella icterica* (n = 64) showed a wider feeding spectrum than *R. crucifer* (n = 30), perhaps because more individu-

Table I. Prey categories with their respective absolute values and relative abundance (N and %N), occurrence (O and %O), volume (V and %V) and index of relative importance (IRI).

	Rhinella icterica							*Rhinella crucifer*						
	N	%N	O	%O	V (mm^3)	%V	IRI	N	%N	O	%O	V (mm^3)	%V	IRI
Arthropoda														
Hexapoda														
Formicidae	1198	74.55	61	100.00	25,775.98	22.92	97.47	559	88.03	27	90.00	7,574.75	51.81	125.86
Hymenoptera non-Formicidae	3	0.19	3	4.92	35.96	0.03	0.01	2	0.31	2	6.67	118.36	0.81	0.07
Coleoptera (adult)	144	8.96	49	80.33	50,876.74	45.24	43.54	30	4.72	15	50.00	3,565.51	24.39	14.56
Coleoptera (larvae)	7	0.44	7	11.48	499.99	0.44	0.10	3	0.47	3	10.00	99.95	0.68	0.12
Diptera (adult)	11	0.68	8	13.11	77.67	0.07	0.10	5	0.79	3	10.00	9.61	0.07	0.09
Diptera (larvae + pupa)	14	0.87	7	11.48	86.56	0.08	0.11	2	0.31	2	6.67	8.40	0.54	0.06
Lepidoptera (adult)	1	0.06	1	1.64	74.86	0.07	0.00	–	–	–	–	–	–	–
Lepidoptera (larvae)	62	3.86	15	24.59	3,494.42	3.11	1.71	4	0.63	4	13.33	279.24	1.91	0.34
Tricoptera (adult)	2	0.12	2	3.28	28.49	0.03	0.00	–	–	–	–	–	–	–
Neuroptera (larvae)	1	0.06	1	1.64	33.46	0.03	0.00	–	–	–	–	–	–	–
Blattaria	45	2.80	27	44.26	18,851.59	16.76	8.67	8	1.26	8	26.67	1948.00	13.33	3.89
Blattaria (oothecae)	1	0.06	1	1.64	28.18	0.03	0.00	–	–	–	–	–	–	–
Isoptera	2	0.12	1	1.64	21.18	0.02	0.00	–	–	–	–	–	–	–
Orthoptera	19	1.18	14	22.95	1,186.88	1.06	0.51	2	0.31	2	6.67	210.27	1.44	0.12
Dermaptera	1	0.06	1	1.64	46.47	0.04	0.00	–	–	–	–	–	–	–
Hemiptera	14	0.87	11	18.03	461.24	0.41	0.23	5	0.79	4	13.33	263.92	1.81	0.35
Plecoptera (naiad)	1	0.06	1	1.64	63.15	0.06	0.00	–	–	–	–	–	–	–
Odonata (naiad)	1	0.06	1	1.64	367.46	0.33	0.01	–	–	–	–	–	–	–
Ephemeroptera	1	0.06	1	1.64	6.67	0.01	0.00	–	–	–	–	–	–	–
Collembola	–	–	–	–	–	–	–	1	0.16	1	3.33	0.54	0.00	0.01
Arachnida														
Opiliones	20	1.24	12	19.67	3,439.63	3.06	0.85	3	0.47	3	10.00	367.84	2.52	0.30
Araneae	25	1.56	17	27.87	2,033.54	1.81	0.94	4	0.63	4	13.33	85.48	0.58	0.16
Crustacea														
Isopoda	4	0.25	4	6.56	328.50	0.29	0.04	–	–	–	–	–	–	–
Myriapoda														
Diplopoda	2	0.12	2	3.28	1,064.61	0.95	0.04	–	–	–	–	–	–	–
Chilopoda	3	0.19	3	4.92	1,191.54	1.06	0.06	–	–	–	–	–	–	–
Annelida														
Oligochaeta	6	0.37	6	9.84	1,165.70	1.04	0.14	–	–	–	–	–	–	–
Hirudinea	–	–	–	–	–	–	–	1	0.16	1	3.33	1.88	0.81	0.07
Mollusca														
Gastropoda	15	0.93	2	3.28	958.14	0.85	0.06	–	–	–	–	–	–	–
Nematomorpha														
Gordioida	–	–	–	–	–	–	–	4	0.63	2	6.67	6.87	0.05	0.05
Skin	2	0.12	2	3.28	–	–	–	1	0.16	1	3.33	–	–	–
Unidentified remains	4	0.25	4	6.56	255.70	0.23	0.03	2	0.31	2	6.67	78.51	0.54	0.06

Table II. Items found in the stomachs of *R. icterica* and *R. crucifer*. (Im) Immature, (*) aquatic.

	R. icterica	*R. crucifer*
Arthropoda		
Uniramia		
Myriapoda		
Diplopoda		
Polydesmida	x	–
Chilopoda	x	–
Hexapoda		
Entognatha		
Collembola	–	x
Insecta		
Hymenoptera		
Formicidae		
Atta	–	x
Acromyrmex	x	x
Brachymyrmex	x	–
Odontomachus	x	x
Camponotus	x	x
Pachycondyla	x	x
Pheidole	x	x
Pseudomyrmex	x	–
Solenopsis	x	x
Brachonoida	x	x
Coleoptera		
Curculidae	x	x
Scarabidae	x	x
Cantharidae	x	–
Pselaphidae* (Im)	x	–
Staphylinidae	x	x
Helodidae (Im)	x	–
Hidrophilidae* (Im)	–	x
Diptera		
Nematocera		
Chaoboridae (Im)	–	x
Chironomidae* (Im)	x	–
Brachycera		
Ephydridae	x	–
Lepidoptera	x	x
Orthoptera		
Gryllidae	x	x
Isoptera		
Termitidae	x	–
Blattaria		
Blattellidae	x	x
Plecoptera		
Perlidae* (Im)	x	–
Dermaptera		
Forficulidae	x	–
Hemiptera		
Auchenorrhyncha		
Cicadellidae	x	x
Membracidae	x	x
Sternorryncha	x	x
Odonata		
Libellulidae* (Im)	x	–
Ephemeroptera		–
Battidae*	x	–
Cheliceriformes		
Chelicerata		
Araneae	x	x
Idiopidae	x	–
Opiliones		
Gonyleptidae	x	x
Crustacea		
Malacostraca		
Isopoda		
Oniscoidea	x	–
Annelida		
Oligochaeta	x	–
Hirudinea	x	–
Mollusca		
Gastropoda		
Basommatophora		
Physidae	x	–
Nematomorpha		
Gordioida	–	x

als of the former were sampled. The most important food items were ants and beetles for both species. Data on the diet of *R. icterica* in the higher-altitude section of Itatiaia National Park (PARNA/I) demonstrated a narrower spectrum, of only five orders. This difference probably is due to prey availability (richness) in a dense ombrophilous forest, such as PARNA/SO, being higher than in high-altitude plains (altitude 2,350 m), such as the higher portion of PARNA/I. Braun (1978) demonstrated that captive individuals of *R. icterica* feed abundantly, readily accepting insects, worms, and a diet based on mice, showing that this species is not selective.

Many authors classify Bufonidae as ant-specialists (Toft 1980, Flowers & Graves 1995, Rosa *et al.* 2002, Isacch & Barg 2002), while others prefer to classify them as generalists (Smith & Bragg 1949, Evans & Lampo 1996, Grant 1996).

The low value of the standardized niche breadth of both species and the disproportionally proportion of ants in the diet suggest that *R. icterica* and *R. crucifer* are specialists. On the other hand, the wide trophic spectrum, particularly in *R. icterica*, contrasts with this conclusion and supports their classification as generalists. ISACCH & BARG (2002) believed that bufonids are ant-specialists, due to their small size and lack of teeth. However *R. icterica* and *R. crucifer* are not small bufonids, and their thick skin (see BRITO-GITIRANA & AZEVEDO 2005) probably makes them more resistant to ant bites and stings, allowing them to feed on these insects for longer periods. TOFT (1980) argued that ant-specialists feed on slow-moving, chitinous prey, whereas non ant-specialists consume more-agile preys. Both species studied herein consumed agile prey such as cockroaches, crickets, and spiders. Further, ants, along with termites, compose approximately 70% of the animal biomass in tropical humid forests (HÖLLDOBLER & WILSON 1990), and Formicidae show eusocial behavior, with the habit of walking on trails, usually in groups. These habits may explain the high numbers of ants found in toad stomachs, and their higher importance in the feeding habits of the anuran species studied. The relatively few records of termites may be due to their cryptic habits, since they travel in tunnels to protect themselves; both individuals found were winged males, which may have fallen to the ground.

Because the trophic-niche breadth values were low and the spectrum was high, we believe that it cannot be said that both species of *Rhinella* are ant-specialists, without knowing all the resources available and applying electivity tests, since in most cases amphibian diets reflect prey availability in the environment (DUELLMAN & TRUEB 1994). ISACCH & BARG (2002) found electivity by ants in *Rhinella arenarum* (Hensel, 1867) and *Rhinella dorbignyi* (Duméril and Bibron, 1841) in the Pampas (lowland plains): DAMASCENO (2005), studying *Rhinella granulosa* (Spix, 1824) in the Caatinga, found positive electivity for ants, and inferred that this preference could be associated with toxin synthesis, a relationship accepted for dendrobatids (CALDWELL 1996). SANTANA & JUNCÁ (2007), also studying *Rhinella granulosa* (Spix, 1824) in the Chapada Diamantina, found positive electivity for isopterans and low electivity for ants.

Beetles were very important in the diets of both species, which corroborates many previous studies (LAJMANOVICH 1994, EVANS & LAMPO 1996, GRANT 1996, ROSA *et al.* 2002), and contrasts with the observations of ISACCH & BARG (2002), who found a negative electivity for this kind of prey, and of SANTANA & JUNCÁ (2007), who found low frequencies for Coleoptera. Although other authors (LAJMANOVICH 1994, EVANS & LAMPO 1996, TEIXEIRA *et al.* 1999, ISACCH & BARG 2002, ROSA *et al.* 2002, SANTANA & JUNCÁ 2007) did not observe cockroaches in the diets of species of *Rhinella*, their abundance, occurrence, and volume were still important in the present study. The presence of aquatic prey, such as Plecoptera and Odonata naiads, an Ephemeroptera sub-imago, mosquito larvae, and some Coleoptera families (Pselaphidae and Hidrophilidae), suggests that *R. icterica* and *R. crucifer* feed in water bodies.

The phylum Nematomorpha belongs to the group Aschelminthes; the larva is a frequent arthropod parasite and the adult is free-living (RUPPERT & BARNES 1996). Although these specimens were found intact, it was not possible to identify their stage of development. In the stomach in which they were found, there were also potential hosts. Because the food items were immediately immersed in 70% alcohol, the possibility that these aschelminths were alive inside the anuran could not be verified.

Most anurans are predators, and probably the plant remains were ingested accidentally, as many workers have suggested (EVANS & LAMPO 1996, TEIXEIRA *et al.* 1999, VAN SLUYS *et al.* 2001). However, LAJMANOVICH (1994), studying *Rhinella schneideri* (Werner, 1894), observed that plant remains collected at the end of the digestive tube, except seeds, showed some signs of digestion. Despite of that observation, this same author believed that the plant remains were accidentally ingested and may have come from leafcutter ants. As related in table II, leafcutter ants (*Acromyrmex* and *Atta*) were also found in the stomachs of *R. icterica* and *R. crucifer*. ANDERSON *et al.* (1999) proposed that ingestion of plant tissue, even without any nutritional value, is not incidental, and help the anuran to avoid parasites and dehydration.

GRANT (1996) observed pieces of plastic in the stomach of *Rhinella marinus* (Linnaeus, 1758); these must have been ingested accidentally, as the plastic pieces and styrofoam were in *R. icterica*. The strong human impact on the area unfortunately exposes the animals to these hazards.

The presence of their own skin in the stomachs of both species corroborates the data collected by EVANS & LAMPO (1996), TEIXEIRA *et al.* (1999), and L.T. SABAGH, who worked with different species of *Rhinella*. WELDON *et al.* (1993) affirmed that this is a common habit in amphibians, which re-use part of their skin during molting. BUSTARD & MADERSON (1965) believed that this is a mechanism used for reclaiming their epidermal proteins.

Although significant, linear regression do not support (r^2 little representative) ontogenetic change in the diet like suggested by some authors for others anuran species.

We conclude that electivity tests are necessary to assess whether the studied species are specialists or generalists and that there is a strong trophic-niche overlap between both species. However, the occurrence of overlap, even to a high degree, does not necessarily mean that competition is present, if the resource is not limited.

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