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Diet, activity patterns, microhabitat use and defensive strategies of *Rhinella hoogmoedi* Caramaschi & Pombal, 2006 from a humid forest in northeast Brazil

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We studied the natural history of the leaf-litter toad, *Rhinella hoogmoedi* Caramaschi & Pombal, 2006, in a rain forest located in an altitudinal rocky remain within the Brazilian caatinga biome. *Rhinella hoogmoedi* was more abundant during the first half of the wet season, when recruitment of new cohorts was observed. Leaf litter was the most commonly used substrate and activity was mainly diurnal. There was a positive relation between maximum prey size (length/volume) and predator size; ants and mites were the predominant prey in adults and froglets, respectively. The following defensive strategies were registered: cryptic and polymorphic colour pattern, immobility, thanatosis, generation of distress calls and production of a foamy substance by the paratoid glands. The similarities in natural history aspects among members of the *R. margaritifera* species group indicate a case of ecological niche conservatism.

Key words: Anura, Bufonidae, foraging ecology, natural history, Rhinella margaritifera

INTRODUCTION

n order to develop appropriate conservation strategies it is necessary to understand the determinants of species distribution and abundance (Child et al., 2008). The choice of which resources to consume may be a result of phylogenetic restrictions, recent ecological interactions or both (Simon & Toft, 1991; Böhning-Gaese et al., 2003; Peltzer et al., 2010). Recent studies highlight the importance of niche conservatism in the life history of species and its implications in ecology, evolution and conservation biology (Peterson et al., 1999; Wiens & Graham, 2005; Wiens et al., 2010). Ecologically, niche conservatism may play an important role in determining traits such as thermo-tolerance, diel activity, habitat preferences and diet (Wiens et al., 2010).

Despite the historical view of anurans as being generalist-opportunistic predators (Wells, 2007), a large array of feeding behaviours from generalist to specialist species has been revealed, including reports of frugivory, geophagy and even consumption of industrialized food (Alexander, 1965; Toft, 1981; McCracken & Forstner, 2006; Silva & Britto-Pereira, 2006). On the other hand, anurans may also be prey for both vertebrate and invertebrate predators (Toledo et al., 2007). Predation is an important factor determining population dynamics (Holt, 1977), affecting life history (Hik, 1995), morphology and behaviour in both ecological and evolutionary timescales (Magnusson & Hero, 1991; Norrdahl & Korpimaki, 2000; Ferrari et al., 2009). In exchange, prey species may use a variety of defensive strategies according to predation phase (localization, identification, approach, subjugation, ingestion and digestion) or to specific predator features (Toledo et al., 2011).

The tropical leaf-litter toad, *Rhinella hoogmoedi* Caramaschi & Pombal, 2006 (Anura: Bufonidae), inhabits leaf litter substrates of forested areas. The species belongs to the *R. margaritifera* species group which comprises 15 species. *Rhinella hoogmoedi* is the only species of the group that occurs in the Atlantic rainforests of Brazil (Caramaschi & Pombal, 2006; Ávila et al., 2010). Despite the studies with this species group over the last 50 years, its taxonomy remains complex and not fully understood (Fouquet et al., 2007; Roberto et al., 2011). Information on ecological aspects of *R. hoogmoedi* is scarce, and restricted to larval and vocal description and a few reports on reproductive behaviour (Caramaschi & Pombal, 2006; Mercês et al., 2009; Roberto et al., 2011).

In this paper we focus on the ecological aspects of *R. hoogmoedi*. More specifically we ask: (i) How does the population structure vary throughout the year? (ii) When are individuals active and what microhabitats are mostly used? (iii) What does *R. hoogmoedi* eat? (iv) Are predator and prey size related? (v) Does diet composition change

ontogenetically or according to the season? (vi) What strategies does it use to avoid predation?

MATERIALS AND METHODS

The study took place at Parque das Trilhas, municipality of Guaramiranga, state of Ceará, northeastern Brazil (04°16'S–38°56'W; 880 m.a.s.l.), 110 km from Fortaleza. Parque das Trilhas occupies an approximately 114 ha, largely continuous tropical moist forest. Guaramiranga has a tropical hot and humid climate and is located in Maciço de Baturité, one of many altitudinal rocky remains that exist within the Brazilian Caatinga biome. The vegetation is characterized by ombrophilous moist tropical rainforest. The mean annual rainfall is 1.676 mm, concentrated between January and May (Funceme, 2010). Average temperatures range from 24–26°C.

We sampled toads visually along forested areas within Parque das Trilhas from April 2009 to June 2010 (details in Brito et al. 2012). Additionally, we inspected five water bodies located near the trails (see Roberto et al., 2011). Each month we conducted time-restrained searches (TRS) for six hours during each diel period (morning: 0800– 1100; afternoon: 1300–1700; night: 1800–2200; two hours per period per day). We used the non-parametric Kruskal-Wallis test to compare frog activity between the three periods (Zar, 1996). For each individual we took notes on microhabitat according to the substrate where it was first observed (e.g., leaf litter, tree trunk, vegetation, streamside, lakeshore, open area or other) and measured snout-vent length (SVL) and mouth width (MW) with digital calipers (precision 0.01 mm).

From July 2009 to June 2010, we assessed the diet of *R. hoogmoedi* by using the stomach-flush technique *in loco* (see Solé et al., 2005). During these encounters, different defensive mechanisms were observed, although logistics did not permit all observations to be quantified. All defensive behaviours observed occurred spontaneously during routine manipulation for stomachflushing and measurement, and animals were not further stimulated (such as in e.g., Hödl & Gollmann, 1986; Toledo et al., 2011). Only individuals with a SVL above 20 mm were stomach-flushed. Forty-five individuals whose SVL were under 20 mm, as well as voucher specimens, were immediately euthanized, fixed with 10% formalin and later transferred to 70% isopropyl alcohol in order to have their stomach-contents extracted by dissection. Food content of each specimen was individually stored in 70% isopropyl alcohol.

Stomach contents were placed on a Petri dish and identified to the lowest taxonomic level (usually order or family) under a stereo microscope. We measured prey length and width using ImageJ software (Abramoff et al., 2004). These measurements were used to calculate prey volume according to an ellipsoid (Magnusson et al., 2003). For each prey category we calculated the frequency of occurrence (*FO*), numerical frequency (*NF*) and volumetric frequency (*VF*). These values were used to calculate the index of relative importance (*IRI*) proposed by Pinkas et al. (1971), as this index strengthens *FO* and *VF*, reducing the bias caused by elevated *NF* associated with single encounters with high density preys.

We used linear regression to investigate the relation between predator size (SVL and MW) and prey variables (maximum/minimum prey length and volume; number of prey per stomach; Zar, 1996). We calculated trophic diversity using Simpson's diversity index and trophic niche breadth using Levin's standardized index (Krebs, 1989).

In order to test for ontogenetic variation in resource consumption, individuals were divided into two size classes: froglets (SVL≤15mm) and adults (SVL>15mm). The threshold of 15 mm for froglets was chosen according to the size of the largest recently metamorphosed individuals found around breeding sites. Numbers of items consumed between size classes and seasons were compared by the non-parametric Mann-Whitney's U test (Zar, 1996). Diet overlap between size classes was calculated using Renkonen's percentage overlap due to its low sensibility to the number of categories into which prey is sorted (Krebs, 1989). To compare prey composition between classes and seasons we calculated a pairwise dissimilarities matrix using Jaccard index and generated a two-dimensional non-metric multidimensional scaling (nMDS) using the metaMDS function of the vegan package in R software. Effects of age and season on diet composition were tested against the final configuration of the nMDS through a multiple two-way ANOVA, with

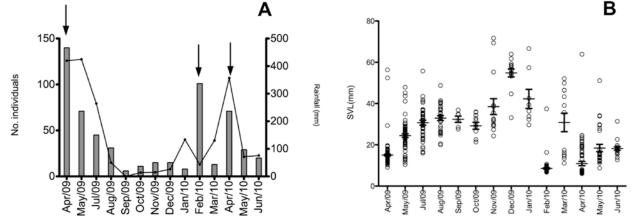


Fig. 1. Relationship between monthly rainfall and abundance (A) and monthly size distribution (B) of *Rhinella hoogmoedi* from the municipality of Guaramiranga, Ceará, in a tropical rainforest in northeastern Brazil.

Table 1. Prey composition of *Rhinella hoogmoedi* from the municipality of Guaramiranga, Ceará, in a tropical rainforest in northeastern Brazil. Categories in italics represent those used in analyses. Values in *italics* represent top three prey categories. Asterisks represent categories with aquatic prey.

	Froglets (n=39)		Adults (<i>n</i> =91)		Total (<i>n</i> =130)	
	NF	IRI	NF	IRI	NF	IRI
Gastropoda	-	-	<0.01	< 0.01	<0.01	< 0.01
Arachnida						
Acarina	0.61	0.83	0.01	< 0.01	0.14	0.05
Araneae	-	-	0.01	< 0.01	<0.01	< 0.01
Anyphaenidae	-	-	< 0.01	< 0.01	<0.01	< 0.01
Araneidae	-	-	< 0.01	< 0.01	<0.01	< 0.01
Salticidae	-	-	< 0.01	< 0.01	<0.01	< 0.01
Theriididae	-	-	< 0.01	< 0.01	<0.01	< 0.01
other	-	-	< 0.01	< 0.01	<0.01	< 0.01
Opiliones	-	-	< 0.01	< 0.01	< 0.01	< 0.01
Myriapoda						
Chilopoda	-	-	< 0.01	< 0.01	< 0.01	< 0.01
Diplopoda	-	-	< 0.01	< 0.01	< 0.01	< 0.01
Crustacea	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
Amphipoda	< 0.01	< 0.01	<0.01	< 0.01	<0.01	< 0.01
Isopoda	-	-	< 0.01	< 0.01	< 0.01	< 0.01
Hexapoda						
Coleoptera	0.06	0.06	0.04	0.04	0.04	0.04
Bruchidae	-	_	< 0.01	< 0.01	< 0.01	< 0.01
Coccinelidae	-	-	<0.01	< 0.01	<0.01	< 0.01
Curculionidae	-	-	0.01	0.01	0.01	< 0.01
Scarabeidae	-	-	< 0.01	< 0.01	<0.01	< 0.01
Staphyllinidae	-	-	<0.01	< 0.01	<0.01	< 0.01
other	0.06	0.06	0.02	< 0.01	0.03	0.01
Collembola	0.06	0.02	<0.01	< 0.01	0.01	< 0.01
Dermaptera	-	_	<0.01	< 0.01	< 0.01	< 0.01
Diptera	<0.01	< 0.01	<0.01	< 0.01	<0.01	< 0.01
Hemiptera	-	-	< 0.01	< 0.01	<0.01	< 0.01
Cydnidae*	-	-	< 0.01	< 0.01	<0.01	< 0.01
other	-	-	< 0.01	< 0.01	<0.01	< 0.01
Hymenoptera						.0101
Formicidae	0.16	0.21	0.84	1.36	0.69	1.04
other	0.01	< 0.01	<0.01	< 0.01	<0.01	<0.01
Isoptera	-	-	0.05	0.04	0.04	0.03
Siphonaptera	<0.01	< 0.01	-	-	<0.01	< 0.01
Larvae	0.06	0.02	0.01	< 0.01	0.02	< 0.01
Coleoptera	-	-	<0.01	< 0.01	<0.01	< 0.01
Diptera*	0.05	< 0.01	<0.01	< 0.01	0.02	<0.01
Tricoptera*	-	-	<0.01	<0.01	< 0.01	<0.01
other	0.01	< 0.01	<0.01	<0.01	<0.01	<0.01
Unidentified prey	0.03	0.01	0.02	<0.01	0.02	<0.01
Plant Material (FO)	-	0.01	0.14	-0.01	0.10	-0.01
Minerals _(FO)	0.28		0.05		0.13	
Simpson's D / Levins' B_{A}	0.59 / 0.14		0.28 / 0.02		0.49 / 0.05	

RESULTS

a Pillai-Bartlet statistic to assess significance. As froglets were only found in the rainy season, comparison between seasons was conducted using only adults. For the same reason, comparisons between froglets and adults were conducted considering only the rainy season. Significance level considered in all analyses was α =0.05. Data are presented as mean±SD (range), unless stated otherwise.

We found a total of 579 individuals of *R. hoogmoedi*, with a mean SVL of 19.87 \pm 12.78 mm (range: 6.02–71.65 mm), and abundance being positively correlated with rainfall (Spearman's *r*=0.59; *p*<0.05; *n*=14; Fig. 1A). Recruitment occurred during the first half of the rainy season (February and April), when froglets were observed on the lakeshore.

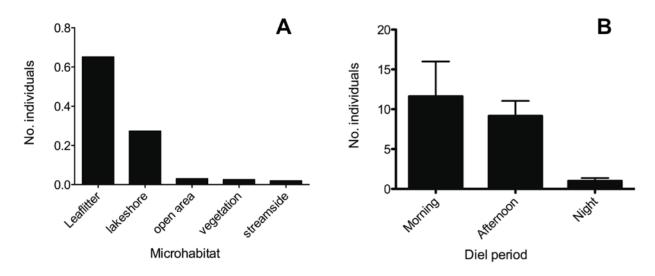


Fig. 2. Variation in relative abundance among different microhabitats (A) and variation in abundance among diel periods (B) of *Rhinella hoogmoedi* from the municipality of Guaramiranga, Ceará, in a tropical rainforest in northeastern Brazil.

After the recruitment period there was an increase on the mean size of frogs, reaching its maximum at the end of the dry season, when reproduction occurred (Fig. 1B).

The most commonly used substrate was leaf litter, accounting for 65.1% of all observations (Fig. 2A). Leaf litter was followed by lakeshore (27.3%), although all individuals (except for one calling male) within this category were recently metamorphosed frogs. Fifteen (2.5%) individuals, apparently inactive, were found using vegetation (e.g., seedling leaves, tree trunks and vines; n=14) and a rope (n=1) as perch sites. Mean perch height was 67 ± 53 cm (15-150 cm). Activity was higher during daytime (0800-1500; H=15.12; p<0.001; Fig. 2B). Although the presence of numerous froglets had a strong influence on the results, this difference was still significant after their removal (p<0.01).

Snout-vent length and mouth width for the 145 individuals of R. hoogmoedi that had their stomachcontents analyzed was 29.12±16.05 mm (6.27 to 71.65 mm) and 10.29±6.57 mm (1.04 to 29.02 mm), respectively. One hundred and thirty individuals (89.65%) had at least one prey item in its stomach. Froglets and adults had similar rates of empty stomachs (9.00% and 10.78%, respectively). A total of 2078 items belonging to 32 categories were identified, with 21 categories being used in the analyses (Table 1). Mean number of prey per stomach was 14.33±16.12 (1-95) and was not related to SVL ($F_{1.128}$ =0.26; r^2 =0.00; p=0.61) or MW ($F_{1.128}$ =0.03; r^2 =0.00; p=0.87). However, we observed a significant difference in the number of prey items per stomach between froglets (11 items/stomach) and adults (18 items/stomach; U=1306; p<0.05). Predator size (SVL and

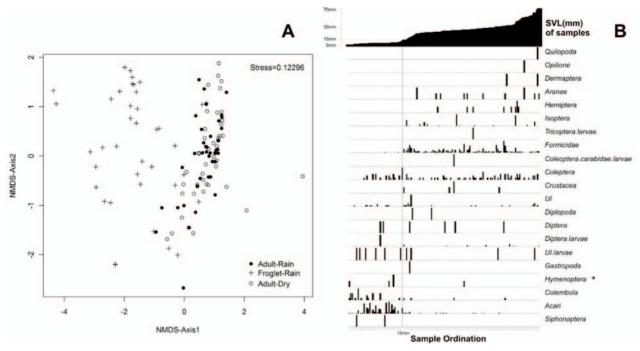


Fig. 3. NMDS ordination of prey classes and seasons (A) and variation in prey composition in relation to body size (B) in *Rhinella hoogmoedi* from the municipality of Guaramiranga, Ceará, in a tropical rainforest in northeastern Brazil.

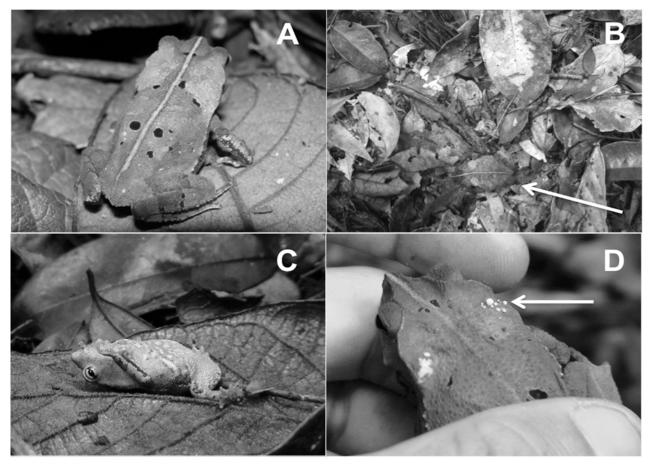


Fig. 4. Defensive strategies observed in *Rhinella hoogmoedi* from the municipality of Guaramiranga, Ceará, in a tropical rainforest in northeastern Brazil. (A) cryptic dorsal pattern; (B) camouflage; (C) thanatosis; (D) secretion of foamy substance.

MW) was positively correlated with all prey parameters analyzed (all p<0.01).

The diet of *R. hoogmoedi* was composed of different invertebrates (Table 1). Overall, ants were the most frequently consumed prey (83.85%), followed by beetles (40.77%) and mites (32.31%). Ants were also the most important prey numerically (69.49%) and volumetrically (48.96%). According to the index of relative importance, ants were the main prey in the diet of *R. hoogmoedi*, with a value twelve-fold higher then the second-most consumed prey (Table 1).

Prey composition amongst size classes was significantly different ($F_{2,126}$ =135.29; p<0.001; Table 1; Fig. 3), with a diet overlap of 24.32%. The diversity of prey and trophic niche breadth in adults (Simpson's D=0.28 and Levin's B_A =0.02, respectively) was narrower than that of froglets (D=0.59; B_A =0.14). Plant material was not found in the stomach of froglets and was present in 14.3% of adults. On the other hand, mineral fragments were present in 28.0% and 5.5% of froglets and adults, respectively.

Number of prey items per stomach did not change significantly between seasons (U=1000; p=0.87). Fifteen out of the twenty-one prey categories analyzed were present in both seasons. Gastropoda, Siphonaptera and larvae of Tricoptera and Coleoptera were only found in the rainy season, while Chilopoda and Opiliones were only detected in the dry season. Despite these differences, we did not detect any significant difference in prey composition between both seasons ($F_{2,126}$ =0.55; p=0.58; Fig. 3).

The most common behaviour observed upon manipulation is that individuals (*n*=53) remain motionless, with legs tucked against the body (Fig. 4C). On a few occasions, individuals would stretch out and stiffen their limbs. The behaviour, interpreted as death feigning or thanatosis (sensu Toledo et al., 2010), would last from 10 s to more than 10 min. We observed distress calls in seven individuals, which were all emitted upon manipulation (calls will be published elsewhere). Four individuals secreted a foamy substance from the paratoid glands (Fig. 4D), which was used as a secondary defensive mechanism in all cases, after either emitting distress calls or feigning dead. Foam was yellowish in the smallest individual (SVL=27.94 mm) and white in the other three (SVL>40 mm).

DISCUSSION

The increase in anuran abundance with the onset of the rainy season is a common pattern (Duellman, 1995; Wells, 2007). The studied population of *R. hoogmoedi* follows this pattern, with higher abundance during the onset of the wet season, when the recruitment of new cohorts was observed. These results contrast with those of other studies with tropical anuran species, including *R.* gr. margaritifera (=Bufo typhonius) (Watling & Donnelly,

2002) in which recruitment occurred mainly in the dry season. Besides annual rainfall distribution, we believe these differences are a consequence of local rain volume. Although adults were found all year, the increase in mean size of *R. hoogmoedi* coupled with the decrease in total abundance throughout the rainy season until the end of the dry season (when reproduction takes place; see Roberto et al., 2011) are indicative of high population cycles and high turn-over rates (Patto & Pie, 2001). Further studies should address this question in more detail, as populations with high turnover rates may be especially vulnerable to stochastic habitat changes (Marsh & Trenham, 2001).

Ninety-three of the adults were observed on leaf litter, making this the most important substrate. In relation to diel activity, 95% of individuals found during TRS were found in the daytime. Individuals spotted at night were frequently perched on vegetation. These patterns are in accordance with other species within the R. margaritifera species complex (e.g., R. gr. margaritifera from Panamá - Toft, 1980b; R. gr. margaritifera from Ecuador and Peru - Toft, 1980a; Ortega-Andrade et al., 2010; R. gr. margaritifera, R. castaneotica, R. magnussoni and R. proboscidae from the Brazilian Amazon - Zimmerman & Bogart, 1988; Caldwell & Araújo, 2005; Lima et al., 2007; R. paraguayensis from Brazilian Pantanal -Ávila et al., 2010). Rhinella hoogmoedi was the most abundant species observed in the leaf litter year-round (other species were: Adelophryne baturitensis, Rhinella crucifer, Physalaemus gr. cuvieri, Ischnocnema gr. ramagii, Leptodactylus mystaceus and Odontophrynus carvalhoi; Brito, pers. obs.). In general, species of the R. margaritifera complex tend to be amongst the most abundant leaf-litter anurans in the areas where they occur, particularly when excluding those with direct development (Duellman, 1995; Poulin et al., 2001; Ávila et al., 2010; May et al., 2010).

The small proportion of empty stomachs observed in *R. hoogmoedi* may be interpreted as a favourable energetic balance in the population (Huey et al., 2001) and an indicator that food is probably not a limiting resource. The lack of a significant relationship between number of prey items and SVL detected for *R. hoogmoedi* has been observed in other species (Duré et al., 2009; Lima et al., 2010). This is expected when one considers that ants (their main prey item) occur clustered in space and that number of individuals consumed will probably depend more on ant species and encounter circumstances than on anuran SVL.

The positive relation between maximum prey size (length/volume) and predator size is a common pattern in different anuran species (Hirai & Matsui, 2002; Teixeira & Vrcibradic, 2003; Bonansea & Vaira, 2007). For animals that swallow their prey whole, mouth width (and consequently SVL) is considered to be a limiting factor in relation to the maximum size of prey consumed (Hespenheide, 1973; Toft, 1980a). Such relation is not expected in animals that specialize on small prey such as mites, ants, termites and flies, where prey is as available to juveniles as it is to adults (Woodhead et al., 2007). Nevertheless, although generally small, ants do vary in size and larger toads are able to eat bigger ants. On the other hand, the positive relationship between minimum prey size and SVL may be interpreted as an indicative that bigger toads are dismissing smaller prey items (e.g., lack of mites or springtails in the diet of individuals with an SVL above 40 mm; Fig. 3B). According to Hirai (2002), such small preys probably represent an insignificant energy source to larger predators.

Although bufonids are generally considered to have ants as their main prey (Clarke, 1974; but see Hirai & Matsui, 2002), some species may change their diet according to its geographical distribution (Bonansea & Vaira, 2007; Suazo-Ortuño et al., 2007). Despite this plasticity, species within the R. magaritifera group demonstrate a clear and stable preference for ants (Toft, 1980a,b, 1981; Lima, 1998; Parmelee, 1999; Maragno & Souza, 2011). The predominance of ants in all measured parameters confirms this tendency for R. hoogmoedi. The few studies on species in the *R. margaritifera* that have identified prey to family show a great similarity not only in ant contribution, but also in secondary items such as coleopteran, with some prey families (e.g., Curculionidae) contributing with a similar proportion, even in species geographically distant (see Toft 1980a, Parmelee, 1999; Maragno & Souza, 2011; this study). An ontogenetic variation in diet was also observed for R. gr. margaritifera in central Amazon by Lima (1998), with smaller individuals having a preference for mites and larger individuals for ants. According to Simon & Toft (1991), smaller anurans are more likely to eat mites, with this tendency being particularly strong in species that specialize in ants, such as Bufonidae. The higher diversity and niche amplitude observed in froglets may indicate a lower degree of specialization within this size class (Bonino et al., 2009).

The presence of plant material has been interpreted as accidental ingestion (Suazo-Ortuño et al., 2007). We believe such material is taken together with leaf-cutting ants, as neither plant remains nor leaf-cutting ants (genus *Atta*) were found in froglets. McCracken & Forstner (2006) suggested geophagy in *R*. gr. *margaritifer* as a mean of absolving toxins from the ingested ants. The presence of mineral remains in *R. hoogmoedi* was likely accidental, as this material was detected in a small proportion of the population and was most frequent in froglets, the class with the least amount of ants in its diet.

The use of low arboreal vegetation as resting sites, especially at night, was also observed in other species of the *R. margaritifera* complex (Zimmerman & Bogart, 1988; Caldwell & Araújo, 2005; Lima et al., 2007). Resting in these sites avoids ground dwelling predators, such as ants, which are frequently present in forested environments (Martins, 1993). In addition, we believe this behaviour may avoid being carried by floods during strong rains, given that most individuals in such retreats were observed in days of intense rainfall (Brito, unpublished data).

Tonic immobility or thanatosis may help prey avoid predation by reducing stimulus in live-prey searching predators, increasing predator distraction in order to escape or allowing an escape opportunity when dealing with predators that stock dead preys (Honma et al., 2006). Given the duration of immobility and the lack of "run-away" attempts, we believe in *R. hoogmoedi* this behaviour is associated with the avoidance of visually oriented predators.

Most species within Bufonidae synthesize and store toxic steroids and biogenic amines that, once secreted by granular glands, provide defense against predators and pathogens (Toledo & Jared, 1995; Daly, 1998). The small amount of individuals observed (*n*=4) to secrete such substances indicates that this strategy is used only under specific circumstances not yet known. Recently Jared et al. (2011) reported the voluntary squirting of poison in *Rhaebo guttatus*. Foam secretion in *R. hoogmoedi* was clearly voluntarily, although not in squirts. Future studies should analyze parotid gland morphology in order to determine its structure and secretion mechanism, permitting further comparison with closely related species (see Jared et al., 2011).

Although very abundant, species in the *R.* margaritifera complex do not appear to be frequently preyed upon. After an extensive literature review we found few reports of predation (*Liophis epinephalus* - Sexton & Heatwole, 1965; *L. reginae* - Albarelli & Santos-Costa, 2010; *Xenoxybelis argenteus* - Menin, 2005; *Ceratophrys cornuta* - Duellman & Lizana, 1994). Poulin et al. (2001) did not find any individual of *R.* gr. margaritifera as prey, although it was the most abundant anuran in the research site. Considering the similar defensive tactics and high local abundance of species in the *R. margaritifera* complex throughout their range, we believe such strategies are not only phylogenetically restrained within this group, but also very effective in predator avoidance.

Conclusions

The natural history traits observed in R. hoogmoedi seem to demonstrate the highly conserved aspect of the ecological niche of species in the R. margaritifera complex, supporting the importance of niche conservatism in species life history (Wiens & Graham, 2005; Wiens et al., 2010). Future studies should analyze how an ecologicalbased phylogeny of the R. margaritifera complex matches the existing ones based on molecular and acoustic data (Fouquet et al., 2007; Roberto et al., 2011). We must first obtain detailed information of its species throughout their range in order to allow a better understanding of the speciation and distribution patterns among this complex group of species. Considering the correlates of foraging mode given in Toft (1981), we found that despite the ant-specialist diet of R. hoogmoedi, it uses both chemical and behavioural defenses, demonstrating the relative plasticity within these patterns. In terms of conservation, this ant-based diet coupled with its micro-habitat use make R. hoogmoedi a good candidate as a bio-agent within agro-forest systems. We believe knowledge on the natural history of species is essential if adequate models are to be constructed, correct predictions are to be made and existing hypotheses are to be adequately tested.

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