

Ecological aspects of the horned leaf-frog *Proceratophrys mantiqueira* (Odontophrynidae) in an Atlantic Rainforest area of southeastern Brazil

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Abstract. This study presents information on habitat use, diet, reproductive aspects of, and the helminth parasite community in, the frog *Proceratophrys mantiqueira* from an Atlantic Rainforest area (APA Mantiqueira) in southeastern Brazil. Frogs were collected at altitudes between 1200 and 1775 m. The estimated population density of *P. mantiqueira* in the area was 2.0 ind/100 m², and the microhabitat most frequently used (82% of the individuals) was the leaf litter on the forest floor. The diet was composed by 20 types of prey items, with Coleoptera and Orthoptera contributing the most important items. The width of the mouth affected the volume of prey consumed by *P. mantiqueira*, as is expected for frogs, because they swallow their prey whole. There were ontogenetic changes in the types of prey in the diet of *P. mantiqueira*, with no ingestion of Coleopteran adults by juvenile frogs (< 26 mm). The clutch size of females of *P. mantiqueira* (692–923 eggs) was similar to those reported for the congeners *P. appendiculata* and *P. tupinamba*, but slightly smaller than those recorded for larger species of *Proceratophrys* such as *P. boiei* and *P. caramaschii*. Despite occurring at relatively low densities in the study area, *P. mantiqueira* had a high prevalence of infection by helminthes (90%), possibly because the helminth parasite community was mostly composed by host-generalists and monoxenous life-cycle species. Diet composition and rates of endoparasite infection, but not microhabitat use, changed with the age structure of the studied populations of *P. mantiqueira*.

Key words. Anura, body size, diet, helminth load, microhabitat, reproductive biology.

Introduction

The life histories of amphibians are highly diverse (DUELLMAN & TRUEB 1994, HADDAD & PRADO 2005). The preference for certain microhabitats in anurans may be influenced by territoriality, food availability, or favourable environmental conditions for breeding and oviposition (CRUMP 1986, PRADO et al. 2005). Diet of an anuran species can be affected by intrinsic (e.g., phylogeny, physiology, ontogeny and sex) and extrinsic (e.g., temporal and spatial changes in food availability) factors, which could lead to dietary differences at population level (BIAVATI et al. 2004, SIQUEIRA et al. 2006, ALMEIDA-SANTOS et al. 2011, DORIGO et al. 2012). Moreover, amphibians tend to host a diverse helminth community, because they use multiple habitats and exhibit a striking diversity of life history patterns, reproductive modes, body sizes, foraging modes, and trophic relations (AHO 1990).

The genus *Proceratophrys* (Odontophrynidae) currently comprises 40 species of terrestrial frogs occurring in

Brazil, Argentina and Paraguay (FROST 2016). Most species of the genus have been categorized into four groups (the *P. appendiculata*, *P. bigibbosa*, *P. boiei*, and *P. cristiceps* groups) based on morphological similarities, although these groups are not supported by phylogenetic analyses (PRADO & POMBAL 2008, CRUZ & NAPOLI 2010, DIAS et al. 2013a, MÂNGIA et al. 2014, MALAGOLI et al. 2016). The *P. appendiculata* group is restricted to the Brazilian Atlantic Rainforest biome and includes species with palpebral appendages and a triangular fleshy rostral appendage (IZECKSOHN et al. 1998, CRUZ & NAPOLI 2010, MALAGOLI et al. 2016); it currently contains 14 species (MALAGOLI et al. 2016) including four recently described taxa previously confused with *P. melanopogon* (*P. mantiqueira*, *P. gladius*, *P. pombali* and *P. itamari*) (MÂNGIA et al. 2014).

Proceratophrys species have a cryptic morphology and coloration that aids in concealing them among the leaf litter (SAZIMA 1978). They are generally found at relatively low densities on the forest floor (GIARETTA et al. 1999, ROCHA et al. 2000, 2007, SIQUEIRA et al. 2009, 2011) during

day and night (ROCHA et al. 2000, 2015). There is still little information regarding ecological aspects such as diet, reproduction, microhabitat or parasitism for these frogs, with data being limited to only eight species (*P. appendiculata*: DIAS et al. 2013b; *P. boiei*: GIARETTA et al. 1998, POMBAL & HADDAD 2005, GIARETTA & FACURE 2008, KLAION et al. 2011, MOURA et al. 2015; *P. caramaschii*: NUNES et al. 2015; *P. goyana*: MOREIRA & BARRETO 1996; *P. mantiqueira*: ALMEIDA-GOMES et al. 2007, MOURA et al. 2015; *P. tupinamba*: BOQUIMPANI-FREITAS et al. 2001, 2002; *P. paviotti*: TEIXEIRA & COUTINHO 2002; *Proceratophrys* sp.: ARAÚJO et al. 2007).

The horned leaf-frog *Proceratophrys mantiqueira* MÂNGIA, SANTANA, CRUZ & FEIO, 2014 is a recently described species endemic to Atlantic Rainforest areas along the Serra da Mantiqueira mountain range in southeastern Brazil (MÂNGIA et al. 2014). Although *P. melanopogon* and *P. mantiqueira* share many morphological characteristics, they differ in some external morphological traits and their advertisement calls (MÂNGIA et al. 2010, 2014). Besides a note reporting egg-laying, in which one captured female had laid 664 eggs (78 eggs were not laid at spawning, totalling 742 eggs) (ALMEIDA-GOMES et al. 2007), nothing is known of the ecology of *P. mantiqueira*.

During a herpetological survey in nine Atlantic Rainforest areas of Rio de Janeiro State, southeastern Brazil, we found individuals of *P. mantiqueira* (see ROCHA et al. 2015, at the time identified as *P. melanopogon*) in one of the surveyed areas. Considering the current scarcity of ecological information about *Proceratophrys* species, we present data on population density, microhabitat use, body size distribution, diet composition, reproductive parameters, and aspects of endoparasitism in that population of *P. mantiqueira*.

Materials and methods

Frogs were collected in the Área de Proteção Ambiental Serra da Mantiqueira (hereinafter APA Mantiqueira; 22°21' S, 44°35' W), an Atlantic Rainforest area in the state of Rio de Janeiro, southeastern Brazil. The study area is characterized by Evergreen Mixed Forest. The climate in this region is wet and warm, with annual rainfall totalling 1813 mm on average, and a mean annual temperature of 14.9°C (maximum 22.9 and minimum 3.7°C) (ATTIAS et al. 2009).

Surveys were carried out in November of 2005 at altitudes between 1200 and 1775 m, using three sampling methods: visual encounter surveys (VES; CRUMP & SCOTT 1994), plots (= squares; JAEGER & INGER 1994), and pitfall traps with drift fences (CORN 1994). During VES, ten people searched for frogs in all periods of the day (daylight hours, dusk and night), totalling 75 hours of sampling effort (25 hours per period). We recorded the microhabitat used by each individual when first sighted. For the plot method, 30 squares of 5 × 5 m (totalling 750 m²) were established during the afternoon and carefully searched at

night; this method allowed us to estimate the local population density (individuals/100 m²) of *P. mantiqueira*. Three pitfall trap systems were used, each consisting of ten 30-litre buckets buried in the ground and set ca. 5 m apart, with soft plastic drift fences about 50 cm high between them. Six buckets were set in line and the other four were placed at opposite ends of the fence, perpendicularly to the main axis. The traps were checked once per day in the morning, during a total of 18 days. All individuals were euthanised with a topical anaesthetic gel (lidocaine 5%), fixed in 10% formalin solution, and preserved in 70% ethylene alcohol. We deposited the frogs in the amphibian collection of the Museu Nacional, Rio de Janeiro (MNRJ 40711–12, MNRJ 40717–40722, MNRJ 51654–51705).

We measured snout–vent lengths (SVL) and jaw widths (JW) of all frogs with callipers to the nearest 0.1 mm. Body mass of the preserved specimens was quantified to the nearest 0.1 g using an electronic scale. We sexed the frogs and considered them adult when males had a SVL greater than 28.4 mm and females had a SVL greater than 36.3 mm (based on MÂNGIA et al. 2014). Frogs captured in pitfall traps were not considered for diet analysis. They were dissected and their stomach contents analysed qualitatively and quantitatively. Animal prey was identified under a dissecting microscope to the level of order, except in the case of Formicidae (identified to family), Gastropoda, and Chilopoda (identified to class). Unidentified arthropod remains were grouped in the “Arthropod Remains” category and considered only for volumetric analysis. For each food item, we measured length and width using callipers (0.1 mm precision), and prey volume (mm³) was estimated using the formula for an ovoid spheroid: $V = 4/3\pi (\text{length}/2) (\text{width}/2)^2$ (DUNHAM 1983). The frequency of each prey category in the diet was expressed as the number of stomachs that contained that category. An index of relative importance (Ix) was calculated for each prey category as the sum of their numeric, volumetric and frequency of occurrence values divided by three (POWELL et al. 1990).

We tested for differences between sexes in SVL of adult frogs using a one-way analysis of variance (ANOVA). To test for differences in jaw width and body mass of the frogs between sexes, we used an analysis of covariance (ANCOVA; with SVL as covariate). We related the number of items per stomach and the volume of the largest prey item ingested with the SVL and the jaw width of the frogs, respectively, using Simple Regression Analyses and disregarding individuals whose stomachs were empty or did not contain identifiable/measurable items (ZAR 1984).

We used a Principal Components Analysis (PCA) to summarize individual variation in diet composition based on volumetric proportions of prey (only prey categories contributing more than 5% of total volume of prey were considered in this analysis). The first principal component was chosen a priori because it summarizes most of the variation in the original data. To analyse ontogenetic shifts in diet composition we used a Spearman Rank Correlation (ZAR 1984) to test the relationship between the first principal component (PC1) and frog size (LIMA & MOREIRA 1993,

GIARETTA et al. 1998). We also analysed sexual differences in PC1 with ANCOVA (with SVL as covariate).

In terms of reproductive aspects, we recorded the total mass of ovarian eggs, the number of mature oocytes, and the diameter of five oocytes taken at random from each ovary (measured with a digital calliper; accuracy of 0.1 mm). We also used previously published data from a clutch obtained during our fieldwork (ALMEIDA-GOMES et al. 2007). Reproductive effort was estimated by dividing the total mass of eggs by the body mass of the respective female (including eggs).

The digestive tract, body cavity, liver and lungs of each individual were checked for endoparasites under a stereomicroscope. The systematic identification of nematodes was carried out following VICENTE et al. (1990), ANDERSON et al. (2009), and GIBBONS (2010). Helminths were temporarily mounted on slides and cleared in Amman's lactophenol for identification. Prevalence (i.e., percentage of infected individuals) and intensity of infection (i.e., average number of parasites per host among infected individuals) were calculated for helminths according to BUSH et al. (1997). The relationship between infection intensity and host size (SVL) was tested with a regression analysis. Helminths recovered were deposited in the Coleção Helminológica do Instituto de Biociências de Botucatu (CHIBB).

Variables were log-transformed whenever the criteria for normality and homocedasticity were not met. Basic statistics shown throughout the text refer to the arithmetic mean \pm one standard deviation.

Results

A total of 60 specimens of *Proceratophrys mantiqueira* (45 males and 15 females) were collected using VES (N = 30), leaf litter plots (N = 15), and pitfall traps (N = 7), and during occasional encounters (N = 8). The population density of *P. mantiqueira* estimated from leaf litter plots in the APA Mantiqueira was 2.0 ind/100 m². The microhabitat most frequently used (82% of the individuals) was the leaf litter stratum on the forest floor (Table 1).

Adult females were significantly larger ($F_{1,37} = 50.79$; $P < 0.001$) than adult males (Table 2). When we excluded the effect of SVL from the analysis, mean jaw width ($F_{1,36} = 0.13$; $p = 0.72$) and body mass ($F_{1,36} = 0.01$; $p = 0.92$) did not differ between sexes (Table 2).

Of the 53 individuals (41 males and 12 females) analysed for diet, fifteen males (or 36.6%) and two females (or 16.7%) had empty stomachs, representing 32.1% of examined individuals. There were no significant differences between sexes in PC1 characterizing diet composition ($F_{1,34} = 0.003$; $p = 0.96$), even when we excluded the effect of SVL from the analysis ($F_{1,33} = 0.57$; $p = 0.45$).

We found 20 types of prey, besides a cocoon and plant remains, in the stomachs of *P. mantiqueira* (Table 3). Coleoptera was, proportionally, the most numerous (22.4%) and voluminous (38.7%) prey item category found. Coleo-

Table 1. Microhabitats used by individuals of *Proceratophrys mantiqueira* (N = 57) in the APA Mantiqueira in southeastern Brazil.

Microhabitat	Frequency (%)
Leaf litter	47 (82.5)
Submerged in stream	3 (5.3)
Fallen tree trunk	3 (5.3)
Edge of stream	2 (3.5)
Root	1 (1.8)
Rock	1 (1.8)

Table 2. Means \pm standard deviation, and range (in parenthesis) of snout-vent length (mm), jaw width (mm), and body mass (g) of *Proceratophrys mantiqueira* (adult males, n = 32; adult females, n = 9; all individuals including juveniles and adults, n = 59 except for snout-vent length where n = 60) from the APA Mantiqueira in southeastern Brazil.

	Snout-vent length (mm)	Jaw width (mm)	Body mass (g)
Adult males	36.4 \pm 2.4 (33.1-40.6)	18.0 \pm 1.2 (16.2-20.0)	5.7 \pm 1.1 (3.7-7.4)
Adult females	46.8 \pm 6.8 (37.2-53.7)	22.8 \pm 3.4 (17.8-26.2)	12.5 \pm 4.8 (5.9-17.4)
All individuals	33.3 \pm 8.9 (14.0-53.7)	16.4 \pm 4.5 (6.5-26.2)	5.2 \pm 3.8 (0.2-17.4)

ptera (41.7%) and Orthoptera (41.7%) were the prey categories most frequently consumed, followed by Coleopteran larvae (25.0%). Coleopteran larvae (V = 12.6%; N = 8.4%) and Orthoptera (V = 10.5%; N = 16.8%) were also volumetrically and numerically important items in the diet (Table 3). Considering the Index of Importance, Coleoptera (Ix = 0.34) was the most important prey category in the diet of *P. mantiqueira*, followed by Orthoptera (0.23) and Coleopteran larvae (0.15) (Table 3). The mean number of prey items per stomach was 3.0 \pm 2.2, varying from 1-13 items. There was no relationship between the number of items ingested and the SVL of frogs ($R^2 = 0.002$; $F_{1,34} = 0.05$; $P = 0.82$), but the volume of the largest prey item was positively correlated with jaw width ($R^2 = 0.39$; $F_{1,34} = 21.68$; $P < 0.001$).

PC1 explained 30.7% of the total variation in diet, and Coleopteran adults had high loadings on this component (loadings: Coleopteran adult = 0.90, "Others arthropods" = -0.65, Orthoptera = -0.50, Coleopteran larvae = 0.22, and Lepidopteran larvae = 0.02). There was a positive and significant relationship between diet composition (PC1) and body size of *P. mantiqueira* ($R_s = 0.27$; $F_{1,34} = 12.58$; $P = 0.001$).

All adult females (N = 7) contained oocytes in their ovaries, and three of them (43%) had mature oocytes. The first of these had 923 oocytes (total mass = 2.5 g; mean diameter of oocytes = 1.8 \pm 0.1 mm; reproductive effort = 14.5%), and

Table 3. Number, volume (V; mm³), frequency of occurrence (F), and Index of Importance (Ix) of prey categories (with percentages in parentheses) in the diet of the frog *Proceratophrys mantiqueira* (N = 36) in the APA Mantiqueira in southeastern Brazil.

Prey category	N (%)	V (%)	F (%)	Ix
Gastropoda	3 (2.8)	10.5 (0.1)	3 (8.3)	0.04
Arachnida				
Acari	2 (1.9)	0.2 (0.002)	2 (5.6)	0.02
Araneae	2 (1.9)	90.3 (0.8)	3 (8.3)	0.04
Opiliones	1 (0.9)	13.4 (0.1)	1 (2.8)	0.01
Malacostraca				
Isopoda	11 (10.3)	162.3 (1.5)	5 (13.9)	0.09
Chilopoda	1 (0.9)	1.1 (0.01)	1 (2.8)	0.01
Hexapoda				
Collembola	1 (0.9)	0.1 (0.001)	1 (2.8)	0.01
Thysanura	1 (0.9)	0.6 (0.01)	1 (2.8)	0.01
Orthoptera	18 (16.8)	1118.2 (10.5)	15 (41.7)	0.23
Isoptera	1 (0.9)	0.1 (0.001)	1 (2.8)	0.01
Blattodea	8 (7.5)	409.5 (3.8)	5 (13.9)	0.08
Hemiptera	4 (3.7)	68.5 (0.6)	4 (11.1)	0.05
Homoptera	1 (0.9)	401.0 (3.7)	1 (2.8)	0.02
Coleoptera (adults)	24 (22.4)	4135.8 (38.7)	15 (41.7)	0.34
Coleoptera (larvae)	9 (8.4)	1351.0 (12.6)	9 (25.0)	0.15
Hymenoptera (Formicidae)	1 (0.9)	2.0 (0.02)	1 (2.8)	0.01
Lepidoptera (adults)	1 (0.9)	27.9 (0.3)	1 (2.8)	0.01
Lepidoptera (larvae)	4 (3.7)	556.5 (5.2)	4 (11.1)	0.07
Diptera (adults)	4 (3.7)	11.5 (0.1)	4 (11.1)	0.05
Diptera (larvae)	4 (3.7)	11.5 (0.1)	2 (5.6)	0.03
Cocoon	1 (0.9)	6.4 (0.1)	1 (2.8)	0.01
Larvae unidentified	4 (3.4)	26.3 (0.2)	4 (11.1)	0.05
Arthropod remains		2026.5 (18.9)		
Seed	1 (0.9)	16.4 (0.2)	1 (2.8)	0.01
Plant remains		191.8 (1.8)	10 (27.8)	
TOTAL	107 (100)	10699,7 (100)	36 (100)	

the second female had 692 vitellogenic oocytes (total mass = 2.0 g; mean diameter of oocytes = 1.8 ± 0.1 mm; reproductive effort = 12.2%). The third female, collected in amplexus, carried 742 eggs (see ALMEIDA-GOMES et al. 2007).

Five species of nematode parasites were found in the frogs: one indeterminate Cosmocercidae, one indeterminate Physalopteridae (larval stage), *Oswaldocruzia lopesi* FREITAS & LENT, 1938 (Molineidae), *Oxyascaris* sp. (Cosmocercidae), and *Rhabdias* sp. (Rhabdiasidae) (Table 4). Parasites were found in the lungs, abdominal cavity, and large and small intestines (Table 4). Overall helminth prevalence for *P. mantiqueira* was 90% (54/60), whereas overall mean intensity of infection was 7.6 ± 5.4 (range 1–24) helminths per host. There was a positive and significant relationship between nematode intensity and host SVL ($R^2 = 0.19$; $F_{1,52} = 12.07$; $P < 0.001$).

Discussion

Population density

Density of *P. mantiqueira* in the leaf litter of the APA Mantiqueira (2.0 ind/100 m²) was higher than densities estimated for other *Proceratophrys* species in Atlantic Forest areas (e.g., 0.2 ind/100 m² for *P. tupinamba* on Ilha Grande – ROCHA et al. 2001; 0.03 ind/100 m² for *P. tupinamba* on Ilha Grande – GOYANNES-ARAÚJO et al. 2015; 0.1 ind/100 m² for *P. boiei* at the Estação Ecológica Estadual Paraíso – ROCHA et al. 2011; 0.3 ind/100 m² for *P. boiei* in the Reserva Ecológica de Guapiaçu – ROCHA et al. 2007; 0.2 ind/100 m² for *P. boiei* in the Serra das Torres – OLIVEIRA et al. 2013). Differences in densities among *Proceratophrys* frogs may be due to local characteristics such as distance from the edge of water bodies (MOURA et al. 2015), depth of the leaf-litter layer in habitat patches (VAN SLUYS et al. 2007), relief and altitude (SIQUEIRA et al. 2011, 2014, GOYANNES-ARAÚJO et al. 2015), and seasonality (GIARETTA et al. 1999, PRADO & POMBAL 2005, GOYANNES-ARAÚJO et al. 2015). These environmental variables should be considered in studies comparing densities of *Proceratophrys* spp.

Microhabitat

Our data indicated that the main microhabitat of *P. mantiqueira* in the forest was the leaf litter on the forest floor, as in other species in this genus (MOREIRA & BARRETO 1996, GIARETTA et al. 1998, BOQUIMPANI-FREITAS et al. 2002, TEIXEIRA & COUTINHO 2002, PRADO & POMBAL 2008). *Proceratophrys* species have a cryptic coloration in relation to the leaf litter, which plays an important role in their camouflage (SAZIMA 1978, PRADO & POMBAL 2008). Moreover, a defensive behaviour of lying flat with legs stretched backwards has been recorded for *Proceratophrys* spp. (SAZIMA 1978, COSTA et al. 2009), which enhances their resemblance of a fallen leaf and increases their potential of protection against visually orientated predators.

Body size

Proceratophrys species have a medium body size (PRADO & POMBAL 2008, MÂNGIA et al. 2014) that will be in general larger than in most of the leaf litter frog species in the Atlantic Rainforest areas (ROCHA et al. 2007, 2011, SIQUEIRA et al. 2009). The largest male (40.6 mm; MNRJ 51663) and female (53.7 mm; MNRJ 51658) of *P. mantiqueira* recorded by us in the APA Mantiqueira were slightly smaller than those recorded by MÂNGIA et al. (2014) for a pooled sample from several localities throughout the species' range, with the largest male measuring 42.5 and the largest female 54.3 mm in SVL. Females are also significantly larger than males in congeneric species such as *P. boiei* (GIARETTA & FACURE 2008), *P. caramaschii* (NUNES et al. 2015), and *P. tupinamba* (BOQUIMPANI-FREITAS et al. 2002). This pattern of sexual size dimorphism is common in amphib-

Table 4. Prevalence (in percentage), intensity of infection (mean \pm SD; with range in parentheses), and site of infection of helminths found in *Proceratophrys mantiqueira* (N = 60) in the APA Mantiqueira in southeastern Brazil.

Helminth	Prevalence (%)	Intensity of infection	Site of infection
Nematoda			
Cosmocercidae indet. (adult)	81.7	4.0 \pm 3.6 (1–15)	Abdominal cavity; large and small intestines
Cosmocercidae indet. (larvae)	1.7	1	Small intestine
Physalopteridae (larvae)	3.3	1	Small intestine
<i>Oswaldocruzia lopesi</i> TRAVASSOS, 1938	1.7	1	Small intestine
<i>Oxyascaris</i> sp.	1.7	1	Small intestine
<i>Rhabdias</i> sp. (adult)	66.7	5.0 \pm 3.3 (1–11)	Abdominal cavity; lung; small intestine

 Table 5. Main prey items of the diet of *Proceratophrys* species, based on proportional number (^N), volume (^V), frequency of occurrence (^F), mass (^M), and Index of Importance (^{I_x}). * EEEP = Estação Ecológica Estadual do Paraíso; REGUA = Reserva Ecológica de Guapiaçu. a – Referred to as *Proceratophrys* sp.; b – as *P. boiei*; c – as *P. appendiculata* in the original publications.

Species	Locality	Items	Reference
<i>P. boiei</i>	EEEP and REGUA, RJ*	Coleoptera, Blattaria, Orthoptera ^{I_x}	KLAION et al. 2011
<i>P. boiei</i>	Atibaia, SP	Coleoptera, Orthoptera ^{N,V,F}	GIARETTA et al. 1998
<i>P. goyana</i> ^a	Serra da Mesa, GO	Coleoptera ^{EM}	MOREIRA & BARRETO 1996
<i>P. mantiqueira</i>	APA Mantiqueira, RJ	Coleoptera adult and larvae, Orthoptera ^{N,V,F,I_x}	This study
<i>P. paviotti</i> ^b	Santa Teresa, ES	Blattaria, Araneae, Lepidoptera larvae ^{N,EM}	TEIXEIRA & COUTINHO 2002
<i>P. tupinamba</i> ^c	Ilha Grande, RJ	Orthoptera ^{N,V,F}	BOQUIMPANI-FREITAS et al. 2002
<i>Proceratophrys</i> sp.	Uberlândia, MG	Blattaria, Insect larvae (terrestrial) ^N	ARAÚJO et al. 2007

ians, except for species in which males engage in intraspecific physical combat (SHINE 1979). Natural selection may promote larger female size, leading to increased fecundity (PRADO & HADDAD 2005, HARTMANN et al. 2010), whereas the smaller size of males may be due to the high energy cost associated with behaviours such as defence of territories and vocalization, and also to different pressures of predation between the sexes, with males having greater exposure to predators as a result of their calling activity (RYSER 1989, LEMCKERT & SHINE 1993). Due to the small sample size of females containing mature oocytes (N = 3) we could not assess the size-fecundity relationship for this population.

Diet

Of the 40 species of *Proceratophrys* currently known, there is information on diet composition for only five of them (= 12.5%; Table 5), including the data of the present study. These data indicate that *Proceratophrys* species feed mostly on Coleopteran adults and larvae, Orthoptera, Araneae, and Lepidopteran larvae (Table 5). These insects have active habits and relatively soft and large bodies when compared to other arthropods commonly found in leaf litter (TOFT 1980a, SANTOS et al. 1998). The ingestion of plant matter was considered an accidental consumption, because

it consisted only of fragments of dead leaves. Because of its moderate body size and presumed sit-and-wait foraging mode (GIARETTA et al. 1998), it might be advantageous for *P. mantiqueira* to focus predation on relatively large and mobile prey, if they are relatively abundant in the habitat, according to the theory of optimal foraging (SCHOENER 1971).

Proceratophrys species apparently avoid Formicidae (MOREIRA & BARRETO 1996, GIARETTA et al. 1998, BOQUIMPANI-FREITAS et al. 2002, TEIXEIRA & COUTINHO 2002, KLAION et al. 2011, present study), even though these insects are commonly dominant among the arthropods living in the forest floor leaf litter (LACERDA et al. 1998, SANTOS et al. 1998). Anurans can be categorized in three general trophic guilds depending on the proportions of different types of prey they consume: ant specialists, non-ant specialists, and generalists (TOFT 1980a). In general, leaf litter frogs are non-ant specialists that will select predominantly soft-bodied, mobile arthropods, mainly orthopterans and spiders (TOFT 1980a,b), as is evident from our study and others on *Proceratophrys* species (Table 5). We do not have data on arthropod availability in the leaf litter in the APA Mantiqueira, so we do not know whether the consumption of those food items by individuals of *P. mantiqueira* is proportional to their availability in the habitat (TOFT 1980a) or whether the frogs will consume these items selectively (TOFT 1980b, HODGKISON & HERO 2003).

Table 6. Clutch sizes of *Proceratophrys* species. Data are shown as presented in the original sources. * Locality not given. a – Referred to as *P. appendiculata* in the original publication.

Species	Locality	Number of oocytes/eggs	Reference
<i>P. appendiculata</i>	Serra dos Órgãos, RJ	656; N = 1	DIAS et al. 2013b
<i>P. belzebul</i> ^a	Ubatuba, SP	355; N = 1	HARTMANN et al. 2010
<i>P. boiei</i>	Atibaia, SP	1296 ± 284; N = 5	GIARETTA & FACURE 2008
<i>P. boiei</i>	Serra de Paranapiacaba, SP	982 ± 199; N = 4	POMBAL & HADDAD 2005
<i>P. caramaschii</i>	Piauí or Ceará *	1200–4300; N = 4	NUNES et al. 2015
<i>P. mantiqueira</i>	APA Mantiqueira, RJ	692–923; N = 3	This study
<i>P. tupinamba</i> ^a	Ilha Grande, RJ	729–946; N=3	BOQUIMPANI-FREITAS et al. 2002

Our data indicated that the size of the mouth affected the volume of prey consumed by *P. mantiqueira*, as it would be expected for frogs because they swallow their prey whole (TOFT 1980a, LIMA & MOREIRA 1993, LIMA 1998, CALDWELL & VITT 1999). A significant relationship between prey size/volume and predator size has also been observed in different frog species from the Atlantic Forest (VAN SLUYS et al. 2001, MARRA et al. 2004, SIQUEIRA et al. 2006), including *Proceratophrys* species, such as *P. boiei* (GIARETTA et al. 1998, KLAION et al. 2011) and *P. tupinamba* (BOQUIMPANI-FREITAS et al. 2002). However, no such relationship was found for *P. moratoi* (ARAÚJO et al. 2007) and *P. paviotti* (as *P. boiei*; TEIXEIRA & COUTINHO 2002).

Our results suggest there may be an ontogenetic shift in the types of prey in the diet of *P. mantiqueira*, with no ingestion of Coleopteran adults by juvenile frogs (< 26 mm). Such relation in the types of prey consumed with SVL has also been recorded for *P. boiei*, in which larger frogs ingested higher proportions of Coleoptera (GIARETTA et al. 1998). On the other hand, no ontogenetic shift in the types of prey consumed was detected in the diet of *P. moratoi* (ARAÚJO et al. 2007). Ontogenetic shifts in the types of prey consumed are probably caused by changes in the preferred prey size (SCHOENER 1971), because the average sizes of individuals vary among arthropod orders (TOFT 1980a, SIMON & TOFT 1991). For at least some species, ontogenetic shifts in the predominantly consumed types of prey may be also explained by ontogenetic changes in foraging activity (LIMA & MAGNUSON 2000) and thus be independent of the electivity for a certain prey size (LIMA & MOREIRA 1993). Because inter-sexual differences were neither detected for *P. mantiqueira* in our study nor for *P. moratoi* (ARAÚJO et al. 2007), we believe that possible behavioural differences between sexes are not important for determining the types of food consumed in the studied species.

Reproduction aspects

The clutch size of *P. mantiqueira* was similar to those reported for *P. appendiculata* and *P. tupinamba*, higher than that reported for *P. belzebul*, and slightly smaller than those recorded for larger species of *Proceratophrys* such as *P. boiei* and *P. caramaschii* (Table 6). Interspecific size-fecundi-

ty relationships in females have been positively correlated with clutch size and egg size regardless of the reproductive mode employed (PRADO & HADDAD 2005). Species with aquatic clutches, such as *Proceratophrys* spp., tend to have larger clutches (HÖBEL 2000, GIARETTA & FACURE 2008) when compared to terrestrially breeding species (WAKE 1978, CANEDO & RICKLI 2006), which helps us to understand the high values recorded by us – almost 1000 eggs per female. The reproductive effort estimated for a female *P. mantiqueira* (14.5%) was similar to that reported for *P. tupinamba* (12.9%; BOQUIMPANI-FREITAS et al. 2002). The measurement of reproductive effort is an important component of many studies on reproductive strategies, because it allows estimating parental investment in courtship and reproduction from the proportional mass (= energy) invested in eggs (DUELLMAN & TRUEB 1994).

Helminth parasite community

We found five species of helminths infecting *P. mantiqueira*, similar to the situation reported for populations of *P. boiei* (KLAION et al. 2011) and *P. tupinamba* (BOQUIMPANI-FREITAS et al. 2001). The relatively low helminth species richness per host population, compared to other vertebrate hosts, was described in previous studies on helminth communities of amphibians (AHO 1990, VAN SLUYS et al. 2006, HALAJIAN et al. 2013). Our study adds one species of Nematoda (*Oswaldocruzia lopesi*) to the list of helminths associated with hosts of the genus *Proceratophrys*, totalling, at least, eight species of Nematoda and one of Cestoda reported for *Proceratophrys* spp. *Oswaldocruzia lopesi* generally infect the stomach and intestines of hosts, and there are previous records of infection by that species in two frog species of the family Bufonidae and in three of the family Leptodactylidae (VICENTE et al. 1990, CAMPIÃO et al. 2014). *Rhabdias* spp. are common lung parasites in amphibians in the Neotropics (ANDERSON 1992, CAMPIÃO et al. 2014). Besides parasitic adults, we found many free-living *Rhabdias* larvae in the frogs' intestines, but as they did not represent parasitic forms, they were not considered (KLOSS 1971, BAKER 1979). Disregarding the larvae of Physalopteridae, all nematode species are monoxenous. The monoxenous helminths contribute to an increased local richness and

prevalence of endoparasites (AHO 1990). *Proceratophrys mantiqueira* represents a new host record for *Oswaldocruzia lopesi*, the genera *Rhabdias* and *Oxyascaris*, and the families Cosmocercidae and Physalopteridae.

Overall helminth prevalence in *P. mantiqueira* (90%) was as high as in *P. tupinamba* (94%; BOQUIMPANI-FREITAS et al. 2001) and higher than in *P. boiei* (60%; KLAION et al. 2011), whereas the intensity of infection in *P. mantiqueira* (mean = 7.6) was similar to that found in *P. boiei* (means of 6.7 and 8.1 in two populations; KLAION et al. 2011). Host SVL explained ca. 20% of the nematode intensity in *P. mantiqueira*, with adults being more parasitised by helminths than juveniles. Juvenile frogs may not have been exposed long enough to acquire the typical adult complement of helminths (AHO 1990). Our result differs from those reported for *P. boiei* (KLAION et al. 2011) and *P. tupinamba* (BOQUIMPANI-FREITAS et al. 2001), because that relationship was not found in these species. As reported herein for *P. mantiqueira*, the body size of individuals significantly affected the number of nematodes found in the Neotropical microhylid frog *Chiasmocleis capixaba*, with larger frogs harbouring more parasites (VAN SLUYS et al. 2006), reflecting the influence of both temporal (time of exposure to potential parasites during life) and spatial (available space inside the host) factors on infection rates (AHO 1990).

Diet composition and rates of endoparasite infection, but not microhabitat use, changed with the age structure of the studied population of *P. mantiqueira*. Juveniles probably segregated in the use of food because of differences in body size per se, foraging activity, and recruitment seasons (LIMA & MAGNUSON 1998). Ontogenetic differences in diet parameters (size and type) may potentially avoid competition in conditions of reduced food availability, but we did not learn if this interaction was important for the evolution of community interactions. Despite occurring at relatively low densities in the study area, *P. mantiqueira* had a high prevalence of infection by helminths, which may be explained, possibly, with helminth parasites of amphibians being mostly host-generalists (AHO 1990).

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