

Sexual dimorphism and resource utilisation by the Veadeiros waterfall frog *Bokermannohyla pseudopseudis* (Anura: Hylidae)

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Abstract. *Bokermannohyla pseudopseudis* is endemic to the Brazilian Cerrado, living in fast-flowing streams in the highlands of northern Goiás State, Brazil. Males have well-developed preopercles and use steady pools in streams for reproduction, and therefore are likely territorial. Along with its small geographic distribution in high-altitude areas and habitat specialization it is a species at risk of extinction. Still, little is known about the ecology of *B. pseudopseudis*, hampering a correct evaluation of its conservation status and possible management strategies. We evaluated resource utilisation and sexual dimorphism in one population to test predictions related to territoriality and to evaluate diet specialization. We found a significant sexual size dimorphism, with males being larger than females, suggesting male-male competition. Males presented thicker forearms whereas females had proportionally longer heads. Tadpoles and calling males are found all year round, suggesting prolonged breeding activity, which is also in accordance with a resource defence breeding structure. Males and females did not select prey by size or volume, but males had wider niche breadths than females. Beetles, spiders, and cockroaches were the most relevant prey items, all of which are commonly found in the habitats of *B. pseudopseudis*. We emphasize that preservation of the habitats of *B. pseudopseudis* is essential to the management of the species because of its microhabitat restriction.

Key words. Amphibia, Brazilian Shield, diet, hypertrophied forearms.

Introduction

Females are larger than males in most frog species (SHINE 1979). This female-biased size dimorphism results from male selection due to the increased fecundity of larger females (WOOLBRIGHT 1983), but may also emerge from age structure dissimilarities due to differences in maturation time and/or mortality rates between sexes (WELLS 2007). Reproductive strategy also is relevant, because size-dependent selection of females seems to be weaker in prolonged breeders (NALI et al 2014), highlighting the influence of reproductive habitat availability in shaping the relationship of male and female body sizes. Conversely, larger males are favoured by sexual selection through male-male competition, female choice, or both (SHINE 1979, SHUSTER & WADE 2003). In amphibians, sexual size dimorphism is

associated with reproductive strategy (WOOLBRIGHT 1983, NALI et al 2014), but the model proposed has been criticized on several grounds (WELLS 2007). Nevertheless, both explosive and prolonged breeding strategies have predictable outcomes for sexual dimorphism.

In prolonged-breeding frogs, males have higher chances of mating, because female receptivity is not synchronized, making them available throughout the breeding season. Hence, aggressive physical encounters between these males should be less common, because they will direct their energy towards acoustically defending territories and attracting females (HÖGLUND 1989, WELLS 2007), which in turn will select males mainly by comparing acoustic signal and territory quality (HALLIDAY 1983). Consequently, sexual selection favours larger males if body size positively affects call characteristics favoured by females (RYAN 1988, RICH-

ARDSON et al. 2010), and/or if territory quality affects female choice (e.g., ROITHMAIR 1994). In some species with prolonged breeding strategies, such as gladiator frogs (e.g., *Hypsiboas boans*, *H. faber*, and *H. pugnax*), males are as large as, or larger than, females (KLUGE 1979, MARTINS & HADDAD 1988). In this group, antagonistic encounters between males are common (MARTINS et al. 1998), and fights between them that can be lethal (KLUGE 1981). Furthermore, territorial behaviour can be energetically demanding and sexual selection may lead to different dietary habits and/or composition between the sexes (e.g., KATSIKAROS & SHINE 1997). Diet quality, on the other hand, can influence body size by affecting reproductive output, development, speed, and survivability (WILBUR & FAUTH 1990, WOOTTON 1992). In this way, territorial males are expected to have a more generalist and opportunistic diet than females, because they will lack the time necessary for selecting prey and have higher energy demands that can constrain a specialized diet.

In explosive-breeding species, males search actively for females, and antagonistic encounters between males are common (WELLS 1977, DAVIS & VERREL 2005). In this case, females are available for mating only during short periods, which is when choruses are formed, and the ability to subdue opponents during antagonistic encounters favours large males. Physical disputes between males commonly occur after the formation of the nuptial pair, and males are expected to differ from females in traits related to amplexic activities, such as forearm width and presence of structures such as spines and nuptial pads (KUPFER 2007, GREENE & FUNK 2009).

Bokermannohyla pseudopseudis is a large saxicolous hylid frog that lives in rocky streams in the sky islands complex of the Brazilian Shield (sensu WARSHALL 1994). Males commonly show scratch marks on their backs and heads, which are generally associated with intrasexual combats in related species (NALI & PRADO 2012, 2014). Indeed, males have well-developed prepollaxes and are generally larger than females. The species presents a limited ability to perch on vegetation and calls from rock outcrops in the riverbed, often close to waterfalls. Herein we evaluate sexual size and shape dimorphism and dietary differences of males and females. Specifically, we were interested in investigating if sexual dimorphism in *B. pseudopseudis* is related to ecological or behavioural constraints.

Material and methods

Sampling

We gathered field data from October of 2007 through January of 2011 in highland Cerrado grasslands in the Alto Paraíso de Goiás Municipality, Goiás State, Brazil. The sampled areas are well preserved and located in, or close to, the Chapada dos Veadeiros National Park, one of the highest areas of the Brazilian Shield, and the type locality of *B. pseudopseudis*. Males were located by active searching, based on their vocalizations. Females were collected opportunistical-

ly and located while moving in the field. In addition, some data were obtained from herpetological collections and previous field notes taken by one of the authors (R.A.B.).

Sexual dimorphism

We used collected and preserved adult specimens (26 females and 47 males in total) for sexual dimorphism analysis. These individuals are deposited in the Coleção Herpetológica da Universidade de Brasília (CHUNB), Coleção Antonio Sebben – Universidade de Brasília (ASUnB), Coleção Zoológica da Universidade Federal de Goiás (ZUFG). Some individuals were collected by R.A.B. and will also be deposited in the CHUNB (field acronym RAB) (Appendix). Their sexes were identified by direct observation of gonads (which were exposed by abdominal dissection) and secondary sex-indicative characters, such as prepollex and nuptial pad development. We measured the following morphometric variables: snout–vent length (SVL), head length (HeL), head width (HW), eye diameter (ED), eye–snout tip distance (ESD), diameter of tympanum (DT), hand length (HaL), forearm length (FrL), forearm width (FW), tibia and foot length (Leg), and femur length (FL). All measurements were taken on the right side of the body using a digital calliper (0.01 mm precision). We $\log_{10}$ -transformed all data to meet normality requirements of statistical tests.

To separate morphometric variation into size and shape variation, we defined an isometric Body Size variable (ROHLF & BOOKSTEIN 1987) following SOMERS (1986): we calculated an isometric eigenvector with values equal to $p^{-0.5}$, where p is the number of variables (JOLICOEUR 1963), and multiplied this $p \times 1$ eigenvector in a matrix $n \times p$ of $\log_{10}$ -transformed data, where n is the number of observations. The result is a vector with one value for each individual (Body Size) that is the sum of all its morphometric measurements. To assess differences in body size between sexes, we conducted an analysis of variance (ANOVA) on the variable Body Size above defined.

For shape analyses, we removed size effects from the $\log_{10}$ -transformed variables with the following procedure (BURNABY 1966): we post-multiplied the $n \times p$ matrix of the $\log_{10}$ -transformed data in a $p \times p$ symmetric matrix, L , defined as:

$$L = I_p - V(V^T V)^{-1} V^T,$$

where I_p is a $p \times p$ identity matrix, V is the isometric size eigenvector defined above, and V^T is the transpose matrix V (ROHLF & BOOKSTEIN 1987). We next applied a logistic regression on the shape variables resulting from the previous procedure to evaluate sexual dimorphism. To assess the statistical significance of the full model based on shape variables, we compared it against a constant-only (null) model using a chi-square test of the scaled deviance (CHAMBERS & HASTIE 1992, FARAWAY 2006). We evaluated each variable's importance for discriminating between sexes by model selection through single-term additions (CHAMBERS & HASTIE 1992): (1) the full model was test-

ed against a constant-only model; (2) the significant term with the lowest Akaike's Information Criterion (AIC) value was added to the null model; (3) step 2 was repeated; (4) any non-significant terms were dropped from the model; (5) steps 3 and 4 were repeated until no more significant terms could be added and no more non-significant terms could be dropped from the model. We then assessed the misclassification error based on the variables selected (reduced model) using 1,000 bootstrap replications of a linear discriminant analysis in the package *ipred* of R v. 2.13.1 (R Development Core Team 2011). We then evaluated the importance of each variable model by averaging and retaining only models with $\Delta AIC_c < 4$ (CRAWLEY 2007), using the MuMIn package (BURNHAM & ANDERSON 2002) of R v. 2.13.1 (R Development Core Team 2011).

Diet analysis

We removed the stomachs of 73 individuals (see Appendix) and analysed their contents under a stereomicroscope, identifying prey to the lowest taxonomic level possible (usually order). The volume of each intact prey was calculated by the ellipsoid formula

$$V_x = \pi \times (L \times W^2)/6,$$

where V_x is the prey volume of item x , L is the prey length, and W is the prey width (MAGNUSSON et al. 2003). To evaluate our sampling of prey, we used the methods of species richness estimation incorporated in EstimateS v. 7.5.1 (COLWELL 2005). Mao Tau was used to represent the smoothing of the observed prey richness, and the Jackknife 1 estimator was used to evaluate stomach content because it is sensitive to space-dependent sampling units (WALTHER & MORAND 1998). We compared differences in Mao Tau estimates for males and females using Z-values.

An index of relative importance (IRI) was calculated for each prey category by using the formula

$$IRI = (N + V) \times F,$$

where N is the numerical percentage, V is the volume percentage, and F is the percentage frequency of occurrence (PINKAS 1971). This method protects against bias that might occur if only N , V or F were used (PINKAS 1971, HART et al. 2002). We calculated niche breadths (B) for numeric and volumetric data as the inverse of Simpson's index of diversity (SIMPSON 1949):

$$B = 1/\sum p_i^2,$$

where p_i is the proportion of occurrence of each category i .

Because a correlation between predator size and prey size is to be expected, we tested whether the largest volume and the largest prey length in each stomach were correlated with each individual's head length (HeL) and head width (HW). To do so, we conducted an analysis of covariance (ANCOVA) with HeL, HW, and sex as predictor variables and prey measurements (item with the greatest length and the greatest volume) as response variables. The purpose of this analysis was to assess whether individuals chose their prey based on size, and to check for sexual differences in prey choice.

Table 1. Summary of morphometric variables of *Bokermannohyla pseudopseudis* according to sex. Values represent mean $\pm$ standard deviation of isometric body size and shape (size-free) variables. Raw values (in mm) are in parentheses.

Variable	Males (N=47)	Females (N=26)
Body Size	3.87 $\pm$ 0.17	3.71 $\pm$ 0.13
Snout-vent length	0.56 $\pm$ 0.02 (53.1 $\pm$ 6.5)	0.58 $\pm$ 0.02 (50.1 $\pm$ 4.5)
Head length	0.12 $\pm$ 0.03 (19.3 $\pm$ 2.3)	0.15 $\pm$ 0.03 (18.7 $\pm$ 4.5)
Head width	0.16 $\pm$ 0.02 (21.5 $\pm$ 2.7)	0.18 $\pm$ 0.01 (19.8 $\pm$ 1.9)
Eye diameter	-0.40 $\pm$ 0.04 (5.9 $\pm$ 0.7)	-0.37 $\pm$ 0.03 (5.7 $\pm$ 1.8)
Eye-snout distance	-0.31 $\pm$ 0.03 (7.2 $\pm$ 0.9)	-0.30 $\pm$ 0.02 (6.7 $\pm$ 0.7)
Tympanum diameter	-0.64 $\pm$ 0.05 (3.4 $\pm$ 0.5)	-0.59 $\pm$ 0.05 (3.5 $\pm$ 0.6)
Tibia length	0.28 $\pm$ 0.02 (27.8 $\pm$ 3.5)	0.30 $\pm$ 0.02 (26.3 $\pm$ 0.5)
Tibia and foot (= leg) length	0.64 $\pm$ 0.02 (63.8 $\pm$ 8.4)	0.66 $\pm$ 0.02 (60.0 $\pm$ 2.9)
Femur length	-0.16 $\pm$ 0.03 (10.2 $\pm$ 1.8)	-0.16 $\pm$ 0.02 (9.2 $\pm$ 0.8)
Forearm width	-0.31 $\pm$ 0.05 (7.4 $\pm$ 1.5)	-0.51 $\pm$ 0.05 (4.1 $\pm$ 0.7)
Hand length	0.07 $\pm$ 0.02 (17.5 $\pm$ 2.1)	0.06 $\pm$ 0.03 (15.1 $\pm$ 2.0)

Results

Sexual dimorphism in size and shape

Morphometric variables are summarized in Table 1. Sexes differed in Body Size ($F_{1,74} = 17.52$, $p < 0.001$) and shape variables ($\chi^2 = 184.34$, $p < 0.001$). Forearm width and head length, in this order, were the most powerful discriminators between the sexes (Table 2). The linear discriminant function using the two selected variables had a misclassification error of 0.0363, based on 1,000 bootstrap replications. The model-averaging analysis retained 35 models with $\Delta AIC_c < 4$; averaged coefficients were significant only for forearm width, which was also the variable with the greatest relative importance (Table 2). Females have proportionally longer heads as compared to males, which for their part have more robust forearms (Table 1, Fig. 1A).

Diet

Rarefaction curves indicate that our collecting effort was quite satisfactory to assess this species' diet richness (Fig. 2A). The rarefaction curves for females only began to reach the plateau (Fig. 2B), possibly indicating a need for

Table 2. Model selection and model averaging of shape variables as predictors of sex in *Bokermannohyla pseudopseudis*. The best model is the shortest model based on manual selection of variables and the Akaike's Information Criterion (AIC). Values represent coefficients of variables in different models. An asterisk indicates a significant model-averaged coefficient ($P < 0.01$). FW – forearm width; HeL – head length; HW – head width; SVL – snout-vent length; DT – tympanum diameter; FrL – forearm length; ED – eye diameter; HaL – hand length; Leg – leg length; FL – femur length; ESD – eye-snout distance.

	Intercept	FW	HeL	HW	SVL	DT	FrL	ED	HaL	Leg	FL	ESD	AIC
Full model	18.20	52.40	-39.39	12.13	13.47	-7.56	4.57	-1.03	16.57	-9.78	-4.26	-3.58	28.94
Best model	26.42	53.59	-33.90	–	–	–	–	–	–	–	–	–	13.00
Model-averaged coefficients	22.83	54.15*	-34.18	22.49	19.17	-8.40	2.51	1.103	16.10	-11.84	1.74	-4.01	–
Relative variable importance	–	1.00	0.90	0.22	0.21	0.20	0.11	0.11	0.10	0.09	0.09	0.09	–

more sampling. Conversely, the dietary sampling effort for males was satisfactory (Fig. 2C). Approximately one third (37%) of the stomachs were empty, suggesting that many individuals had not been preserved quickly enough after collection (most of the specimens from herpetological collections). After excluding juveniles and empty stomachs, we were left with prey found in 33 males and 13 females. We identified 91 items, excluding plants, unidentified arthropods, and digested items. These unidentified items were also quantified (Table 3), but they were not included in the calculation of niche breadth, ANCOVA, or rarefaction curves. Although there are no significant differences between male (M) and female (F) diet rarefaction curves ($Z_M = 2.897$, $Z_F = 1.505$, $p = 0.058$), male dietary composition tends to be broader than female. Differences based on rarefaction curves are more affected by the less-sampled curve (GOTELLI & COLWELL 2001); thus, dietary differences between male and female *B. pseudopseudis* could be significant if a larger sample of females were used. However, the most important items were the same for both sexes, except Heteroptera, which were commonly found in females but not in males (Table 3).

The ANCOVA results indicate a high randomness in prey size (Table 4), suggesting that larger individuals do not necessarily choose larger prey.

Discussion

Males of prolonged-breeding species acoustically defend a territory and rarely engage in physical combats (WELLS 1977). Still, some species, such as true gladiator frogs (sensu FAIVOVICH et al. 2005), have a prolonged breeding season, but are territorial and engage in territorial fights. This seems to be the case in *B. pseudopseudis* as well, given the presence of hypertrophied spiny prepollexes (POMBAL JR. & CARAMASCHI 1995) and scratch marks on male's backs (Fig. 1B). If sexual size dimorphism is really indicative of sexual selection in *B. pseudopseudis*, males nevertheless defend a territory, whereas females may select mates by territory quality, conforming to NALI & PRADO (2012, 2014) who recorded strong territoriality and fights in *B. ibiti-guara*. On the other hand, SAZIMA & BOKERMANN (1977) never observed more than three males of *B. alvarengai* along 400-m transects on streams. Both species are phylogenetically related with *B. pseudopseudis* (FAIVOVICH et al. 2005).

Hypertrophied forearms and prepollex spines, however, are also directly involved in amplexus (HEYER 1969, GREENE & FUNK 2009). Therefore, the enlarged forearms and prepollexes of *B. pseudopseudis* males could be solely a response to amplexus requirements. For example, HEYER

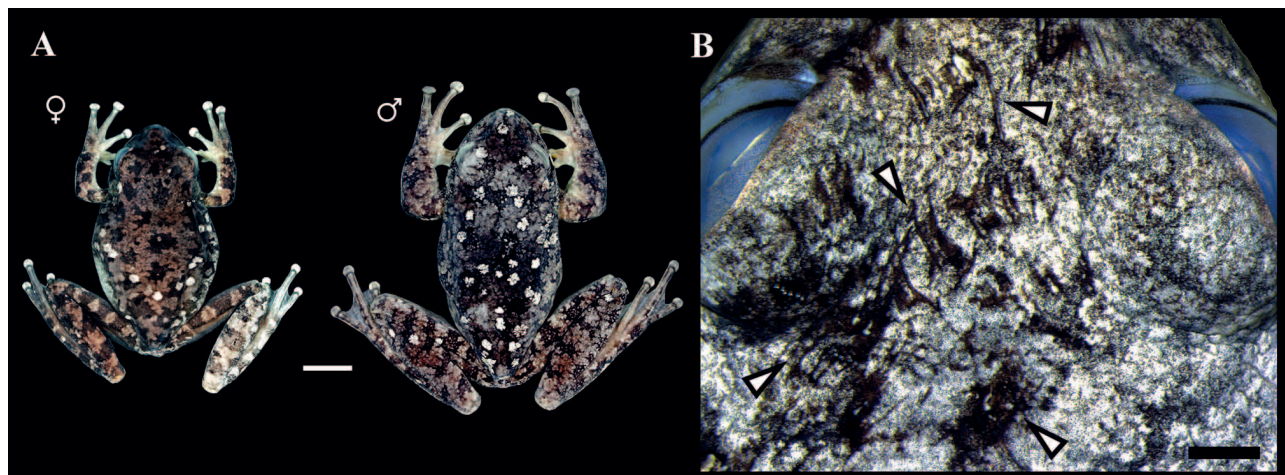


Figure 1. A) Female and male of *Bokermannohyla pseudopseudis*, illustrating male-biased sexual size dimorphism; B) scratch marks on a male's head. White arrowheads indicate some scarred areas, white bar – 1 cm and black bar – 2 mm.

Table 3. Diet composition of males and females of *Bokermannohyla pseudopseudis*. N – total number of the item recorded; F – frequency of each prey category in stomachs; V – total volume of item category; IRI – index of relative importance.

Prey category	Male (n = 33)							Female (n = 13)						
	N	N (%)	F	F (%)	V (cm ³)	V (%)	IRI	N	N (%)	F	F (%)	V (cm ³)	V (%)	IRI
Araneae	8	11.59	8	14.04	1028.51	10.84	314.91	11	31.43	2	9.09	101.92	3.25	315.25
Blattaria	5	7.25	5	8.77	2224.36	23.45	269.27	4	11.43	2	9.09	104.73	3.34	134.24
Coleoptera	21	30.43	12	21.05	1812.36	19.10	1042.90	7	20.00	5	22.73	327.52	10.44	691.79
Diptera	3	4.35	2	3.51	14.28	0.15	15.78	–	–	–	–	–	–	–
Ephemeroptera	2	2.90	2	3.51	130.74	1.38	15.01	–	–	–	–	–	–	–
Hemiptera (Heteroptera)	–	–	–	–	–	–	–	2	5.71	2	9.09	576.11	18.36	218.87
Hemiptera (Homoptera)	4	5.80	3	5.26	269.44	2.84	45.46	–	–	–	–	–	–	–
Hymenoptera (Formicidae)	5	7.25	5	8.77	142.69	1.50	76.76	2	5.71	2	9.09	11.32	0.36	55.23
Isoptera	1	1.45	1	1.75	4.55	0.05	2.63	–	–	–	–	–	–	–
Lepidoptera (larvae)	5	7.25	4	7.02	2695.20	28.41	250.25	1	2.86	1	4.55	473.61	15.09	81.60
Mantodea	1	1.45	1	1.75	54.56	0.58	3.55	–	–	–	–	–	–	–
Orthoptera	3	4.35	3	5.26	532.21	5.61	52.41	–	–	–	–	–	–	–
Unidentified arthropods	4	5.80	4	7.02	34.14	0.36	43.21	3	8.57	3	13.64	0.87	0.03	117.26
Plants	5	7.25	5	8.77	414.33	4.37	101.88	3	8.57	3	13.64	89.15	2.84	155.63
Unidentified items	2	2.90	2	3.51	128.34	1.35	14.92	–	–	–	–	–	–	–
Total	69				9485.35			33				1685.24		

Table 4. Prey selectivity (size and volume) based on head size and sex of individuals of *Bokermannohyla pseudopseudis*. All probability values (p) indicates high randomness in models. df – degree of freedom.

Effect	Longest item			Most voluminous item		
	F	df	p	F	df	p
Head length	0.02	1.00	0.88	0.56	1.00	0.46
Head width	0.00	1.00	0.97	0.08	1.00	0.78
Sex	0.20	2.00	0.82	0.25	2.00	0.78

(1969) showed that the presence of these secondary sexual characters in *Leptodactylus* is related to species' habits, with these traits being more pronounced in aquatic species, be-

cause females are very slippery and a secure amplexic hold is the key. *Bokermannohyla pseudopseudis*, however, is not aquatic and females are not slippery, but we still cannot discard this hypothesis.

Male fights in riparian anurans may be associated with the territorial defence of limited oviposition sites in streams (TSUJI & MATSUI 2002, KUPFER 2007). *Bokermannohyla pseudopseudis* likely shelters its eggs in rock crevices or under stones in the manner reported for *B. saxicola* (ETEROVICK & BRANDÃO 2001). Because males were found calling alone in waterfalls and tadpoles live and thrive in backwaters immediately below them, SHINE's (1979) hypothesis of male-biased sexual dimorphism associated with territorial defence seems corroborated. Behavioural observations and/or experiments will likely be paramount to picking the hypothesis that explains sexual dimorphism in this spe-

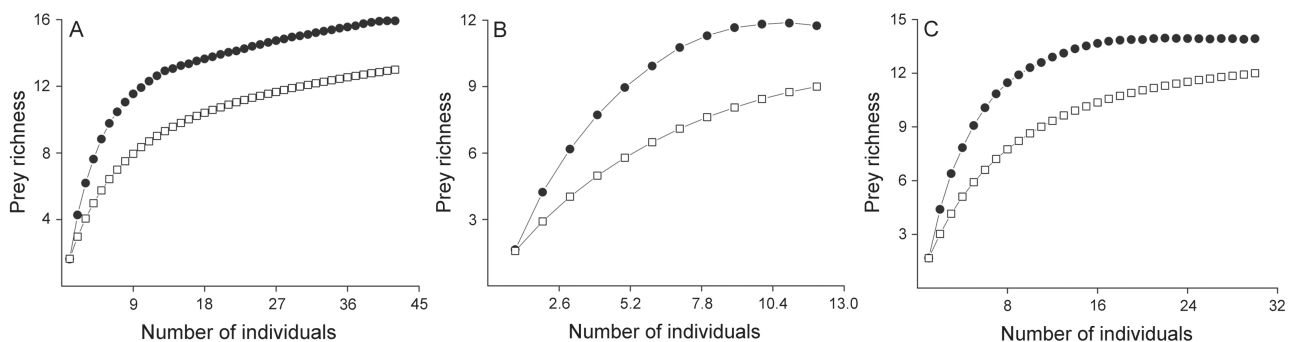


Figure 2. Rarefaction curves of observed and estimated diversity of prey items ingested and accumulated by individuals. A) global (males + females + juveniles); B) female; C) male. Open squares – observed richness (Mao Tau) and black circles – estimated richness (Jackknife 1).

cies best (see observations made by ROITHMAIR [1994] and KATSIKAROS & SHINE [1997]).

The diet of *B. pseudopseudis* may be explained by a trade-off between times spent on territory defence and prey selection. Males must feed on any prey present in their territory, regardless of volume and energetic content (LUCAS 1985). Indeed, our results marginally support the idea of a more specialized diet in females. Females may be able to select prey more efficiently, because they do not need to defend territories. This adds support to the hypothesis of territorial defence by males. The generalist diet of *B. pseudopseudis*, in contrast, may be associated with its distribution.

Species with small geographic ranges are usually generalists, a trend that may result from extinction risk shaping species richness (WILLIAMS et al. 2006). This risk is much greater for narrowly distributed species with specialized diets (JOHNSON 1998). As generalist predators often predominantly consume the most abundant prey in their habitats (SIH & CHRISTENSEN 2001), *B. pseudopseudis* may consume mainly terrestrial arthropods present along rocky streams. The most important items in the diet of *B. pseudopseudis* were beetles (Insecta, Coleoptera), long-jawed orb weavers (Arachnida, Tetragnathidae), wolf spiders (Arachnida, Lycosidae), and terrestrial cockroaches (Insecta, Blattaria). These arthropods are common in the rocky situations along rivulets in Chapada dos Veadeiros. Wolf spiders are cursorial, long-jawed orb weavers that make cobwebs next to, or in, rock crevices. It is common to spot these webs covered with dew or spray from waterfalls (R.F.M. pers. obs.).

An important aspect for *B. pseudopseudis* conservation and management is the fact that, although the species is a feeding generalist, it depends on certain reproductive sites and has a small geographic range. Hence, the persistence of the species depends on the preservation of the highland rocky streams where it occurs and a management that is adequate for conserving riverine habitats that are subjected to human activities, such as farming and tourism.

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Appendix

List of specimens examined

Males: CHUNB: 8524, 14065, 14367, 14368, 14389, 14395, 17527, 17532, 43650, 47516, 58791, 58792, 58794, 58873, 58874, 58876, 58879, 59085, 59086, 62502, 62511, 62514–62520, 62523–62528; ASUnB: 2582; ZUGF: 2062, 2072, 2623; RAB: 2892, 2901, 2902, 2916, 2920, 2943, 2945, 2967.

Females: CHUNB: 14382, 14385, 14394, 17528, 17531, 28957, 32619, 42522, 47515, 49511, 58789, 58793, 58872, 58875, 59087–59090, 62513, 62521, 62522, 62529; ZUGF: 2061; RAB: 2906, 2919, 2944.