Ecology of *Hypsiboas albopunctatus* (Anura: Hylidae) in a Neotropical Savanna

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Abstract.—Although the treefrog *Hypsiboas albopunctatus* (Spix, 1824) (Anura: Hylidae) is abundant in South America, especially in regions of open vegetation in Brazil, information regarding its natural history is still scarce. This study describes its ecology including aspects of microhabitat use, population dynamics, diet, and reproduction in the Cerrado biome of central Brazil. We used model selection to test hypotheses of variation in survival and recapture rates as a function of differences in sex, seasonality, and climatic variables. We also tested hypotheses regarding sexual dimorphism. This species uses mainly herbaceous vegetation and bushes along margins of the ponds. Apparent survival, estimated using the Cormack-Jolly-Seber mark-recapture model, was higher for males than females and was negatively correlated with rainfall. Recapture probability was influenced by seasonality, presenting higher values in the wet season. This highlights the influence of weather, especially seasonal rainfall, on the population dynamics of anurans occurring in tropical savannas. The analysis of previously preserved individuals showed strong sexual dimorphism in body size and shape, with females being larger than males. Female body size positively correlated with clutch volume. *Hypsiboas albopunctatus* seems to have a generalist diet, consuming primarily Coleoptera, Aranae, and Orthoptera (assuming accidental vegetal ingestion). Prey size was positively correlated with anuran head size. *Hypsiboas albopunctatus* seems to be a generalist, as demonstrated by its continuous activity and reproduction, generalist diet, and habitat use, presenting some breeding adaptations to enhance offspring size, such as sexual size dimorphism related to clutch volume in females.

The Brazilian Cerrado is one of the world's largest biodiversity hot spots (Myers et al., 2000). Threatened by the increasing demand for land used in agriculture and raising cattle, >50% of its area has been devastated over the past 35 years (Klink and Machado, 2005). This Neotropical savanna is characterized by well-defined wet and dry seasons and is composed of heterogeneous vegetation, ranging from grasslands to dense gallery forests, with a predominance of savanna vegetation (Oliveira-Filho and Ratter, 2002; Ribeiro and Walter, 2008). Amphibian species occurring on this habitat are usually greatly influenced by the Cerrado climate with rain and temperature among the most important variables influencing both reproduction and activity (Colli et al., 2002; Vasconcellos and Colli, 2009). Also, because these animals are ectothermic and have permeable skin, there is usually a strong relationship between environmental variables and their biology. Thus, these characteristics and physiological needs leave them vulnerable to environmental changes affecting their individual survival and population dynamics.

Studies about the geographic distribution, natural history, and ecology of Neotropical amphibians are very scarce (Silvano and Segalla, 2005), so even basic information about the natural history of the Cerrado herpetofauna is still lacking (Colli et al., 2002). Furthermore, the worldwide decline in amphibian populations has highlighted the importance of studies about their population ecology and reproduction to understand the factors that affect their survival, especially in poorly known regions (Kiesecker et al., 2001; Silvano and Segalla, 2005).

Hypsiboas albopunctatus (Spix, 1824) (Anura: Hylidae) is a broadly distributed treefrog in South America (Frost, 2010). In Brazil, it is mostly found in open vegetation habitats throughout the central and southern regions (Frost, 2010). To assist conservation efforts, ecological data and demographic studies are needed to better understand the factors shaping the ecology of anuran species in tropical savannas (Alford and Richards, 1999; Silvano and Segalla, 2005). This study describes aspects of the biology of *H. albopunctatus* in the Cerrado of central Brazil, including microhabitat use, survival, sexual

dimorphism, reproduction, and diet. Herein, we test hypotheses of variation in survival and recapture rates explained by differences in sex, seasonality, and climatic variables such as temperature and rainfall. We also evaluate the morphometric dimensions of this treefrog for a relationship with relative prey size and to determine whether there are morphological differences between males and females (sexual dimorphism) and whether any difference are consistent with an optimization of female body size relative to clutch size or volume.

Materials and Methods

Study Site, Habitat, and Microhabitat Use.—Our study was conducted in a permanent artificial lake, with a trapezoid shape, in the Cerrado biome of central Brazil near the city of Gama (16°01′S, 48°12′W), Distrito Federal. The lake had its margins divided into four transects (along the shore) according to shoreline habitat type: A, margin with herbaceous vegetation and bush; B, margin with the exotic grass *Brachiaria* sp.; C, steep margin with little vegetation; and D, gallery forest, near Acém spring, which fills the lake. Transects A, B, and C were the same length, ≈40 m, and transect C was ≈15 m.

The population was studied over 24 consecutive months, from March 2006 to February 2008, with sampling events occurring once a month, over three consecutive nights. Once the treefrogs had started calling after sunset, the vegetation along the shore of each transect was visually surveyed by three researchers for ≈5 h by using a flashlight. Visual encounters and audio strip transects were used to locate frogs (see Heyer et al., 1994). Individuals were captured by hand, immediately checked for previous markings, marked if not previously captured, and released in the same place. After capture, their habitat (transect) and microhabitat data also were recorded, and microhabitat categories included water, ground, grass, bush, and tree (plants >3 m). Sex was determined based on vocalization and presence of a vocal sac in reproductive males. Only adults were used in the analysis because of the sparseness of juvenile captures.

Demographic Analysis.—Each frog was individually marked by toe clipping. Although we cannot disregard the possible negative effects this marking technique may have on survival of treefrogs (Waddle et al., 2008), this method is reported to

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cause less stress than other marking methods (Langkilde and Shine, 2006). Therefore, we do not believe this methodology invalidates the assumptions of our demographic analysis.

Mark-recapture data were used to estimate demographic parameters, such as apparent survival (φ) and recapture probability (*p*), estimated monthly over the study period. We used the Cormack-Jolly-Seber (CJS) model for open populations in MARK 5.1 (White and Burnham, 1999). Because in open populations permanent emigration cannot be distinguished from mortality, the CJS model produces an estimate of apparent survival (φ). The CJS model is based on the assumptions of (1) equal probability of marked animals being recaptured during one sampling occasion, (2) equal probability of marked animals surviving from a particular sampling time to the next, (3) marks not lost or missed, and (4) instantaneous sampling of individuals with immediate release relative to the interval between samples (Krebs, 1999). Assumptions 1 and 2 (test 2 and test 3) were evaluated using the goodness-of-fit (GOF) test in U-CARE, version 2.2 (Choquet et al., 2002). Based on our protocol, we believe assumptions 3 and 4 were not violated.

We started the search for parameters in the model explaining the variation in apparent survival and recapture probability of *H. albopunctatus* by using the most global model with the maximum number of parameters, φ(s*t) *p*(s*t), where both φ (apparent survival) and *p* (recapture rate) can have different values for each sex (s) and vary freely with time (t) with a different estimate each month. After confirming the validity of the global model via GOF tests, alternative models with fewer parameters were generated to verify the importance of the variation according to sex and time on these estimates. The model selection procedure itself can be an important method of hypothesis testing for factors influencing survival and recapture of individuals and in the acquisition of the best estimates for apparent survival and recapture. We fit models and performed model selection based on Akaike's information criterion for small sample sizes (AICc) (Mazerolle, 2006). The AICc value and the Akaike weight (W$_{\text{AIC}_C}$) are used to determine which models have the most support. The best model, the model with the lowest AICc value, provides good fit to the data with the fewest parameters possible. W$_{\text{AIC}_C}$ describes the relative strength of the evidence in support of a particular model, or the probability that a given model is the best one compared with other models.

Model selection was performed following the procedure of model building and selection described in Lebreton et al. (1992) by using three main steps. (1) We tested all the possible nested models of the global model constraining sex or time variation one at a time or two at a time in the survival and recapture parameters to evaluate the variation of these parameters. This way, we generated 15 preliminary candidate models with fewer parameters than the global model, and the best model of survival in this preliminary set was used as a starting point to test hypotheses of variation for recapture rate. (2) We tested the effect of climatic variables (average daily rainfall and temperature for each month) in explaining the variation in recapture rates. Recapture probability was set as a linear function of these climatic variables. We also tested the effect of seasonality, assuming different recapture probabilities for dry and rainy seasons. (3) After achieving the best model for recapture probability, necessary to avoid bias and imprecise survival estimates, we started testing hypotheses of variation in survival. We tested the effects of monthly average rainfall and temperature and also the effect of seasonality for survival, in the same way we did for recapture rate. Monthly climatic data were obtained from the IBGE Meteorological Station located 20 km from the sampling site.

We derived apparent survival and recapture estimates using the model-averaging approach, accounting for the uncertainty of each model. This approach uses the W$_{\text{AIC}_C}$ of each candidate model to derive a weighted-average estimate for each parameter of survival and recapture, deriving more accurate estimates (for details, see Burnham and Anderson, 2002).

Sexual Dimorphism.—We dissected individuals previously deposited at the Coleção Herpetológica da Universidade de Brasília (CHUNB) from different localities in the states of Goiás and Distrito Federal, Brazil. Sex was determined by observing the presence of ovaries or testes. For each individual, we measured snout–vent length (SVL), head width, head length, tibia length, foot length, forearm length, tympanum diameter, and eye diameter with electronic calipers to the nearest 0.01 mm.

We log$_{10}$-transformed all morphometric variables prior to analyses to meet the requirements of normality (Zar, 1998). To partition total morphometric variation between size and shape variation, we defined body size as an isometric size variable (Rohlf and Bookstein, 1987) following the procedure described by Somers (1986). This method is based on a principal component analysis and is very useful in avoiding using a one-dimensional body size variable, such as SVL. We calculated an isometric eigenvector, defined a priori with values equal to $p^{-0.5}$, where p is the number of variables (Jolicoeur, 1963). Next, we obtained scores from this eigenvector, hereafter called body size, by post-multiplying the n by p matrix of log-transformed data, where n is the number of observations, by the p by 1 isometric eigenvector. To test the null hypothesis of no difference between sexes, we conducted separate analyses of variance on body size (analysis of variance [ANOVA]) and the shape variables (multivariate analysis of variance [MANOVA]) by using log$_{10}$-transformed data.

Reproduction.—The same individuals used for sexual dimorphism analyses had their reproductive condition evaluated. Females were considered reproductive when their ovaries were convoluted and enlarged, or when developed eggs were present. All eggs were removed and counted, and the diameters (*d*) of five eggs from each female were measured with electronic calipers and a magnifying glass. Egg volume was estimated using the formula for a sphere:

$$V = \frac{4}{3}\pi\left(\frac{d}{2}\right)^3.$$

Linear regressions were performed to verify the existence of correlation among SVL vs. clutch size, clutch volume, and egg volume.

Diet Composition.—Dissected individuals had their stomachs removed and prey items were identified to order taxonomic level. The length and width of intact prey were recorded with electronic calipers to estimate prey volume as an ellipsoid:

$$V = \frac{4}{3}\pi\left(\frac{w}{2}\right)^2\left(\frac{l}{2}\right),$$

where w is prey width and l is prey length. The numeric and volumetric percentages of each prey category for individual and for pooled stomachs were calculated.

To determine the importance of individual stomach and pooled stomachs of each prey category, the following formula was used:

$$I = \frac{F\% + N\% + V\%}{3},$$

where $F\%$ is the occurrence percentage, $N\%$ is the numeric percentage, and $V\%$ is the volumetric percentage.

To investigate the relationship between prey size and frog head measurements, a canonical correlation analysis was used with two sets of variables: maximum prey length and width vs. frog head length and width. We carried out statistical analyses

TABLE 1. Top candidate CJS models for monthly apparent survival (φ) and monthly recapture rate (p) for *Hypsiboas albopunctatus*, considering effects of sex variation (s), rainfall (rain), temperature (temp), seasonality (wet/dry), additive effects of sex and rain (s+rain), interactive effects of sex and rain (s*rain), or no variation (.). AICc =Akaike's information criterion for small samples; ΔAICc = difference of AICc between any model and the best model; W_{AIC_C} = Akaike's weight of fit for each model; K = number of estimated parameters.

Models	AICc	ΔAICc	W_{AIC_C}	K	Deviance
φ(s+rain) p(wet/dry)	497.11	0	0.53	5	254.810
φ(s*rain) p(wet/dry)	499.23	2.12	0.19	6	254.805
φ(s) p(wet/dry)	500.40	3.29	0.10	4	260.201
φ(rain) p(wet/dry)	502.11	5.00	0.04	4	261.913
φ(s) p(.)	502.86	5.75	0.03	3	264.739
φ(wet/dry) p(wet/dry)	503.72	6.61	0.02	4	263.525
φ(.) p(s)	503.79	6.68	0.02	3	265.674
φ(s) p(temp)	504.26	7.15	0.02	4	264.059
φ(temp) p(wet/dry)	504.37	7.26	0.01	4	264.175
φ(s) p(rain)	504.71	7.60	0.01	4	264.511
φ(s) p(s)	504.88	7.77	0.01	4	264.680
φ(.) p(wet/dry)	505.00	7.89	0.01	3	266.885

using SYSTAT 12.0 for Windows, with a significance level of 5% to reject null hypotheses. Means are given ± 1 SD.

RESULTS

Microhabitat Use.—Of the 213 captures, 163 (76.5%) individuals were found on bushes; 6 (2.8%) in the water; 33 (15.5%) on the ground; and 11 (5.1%) in the grass. No individual was captured in trees. We detected more frogs on transect A (margin with herbaceous vegetation and bush) with 104 captures (49%), followed by transect C (steep margin with sparse vegetation) with 50 captures (23.4%), transect B (margin with exotic grass *Brachiaria* sp.) with 41 (19.2%), and transect D (gallery forest, near the spring) with 18 captures (8.4%).

Demographic Analysis.—Over 24 months of study, 153 individuals of *H. albopunctatus* were marked, of which 62 were recaptured, for a total of 213 captures. We marked 137 males and 16 females in total, with a biased sex ratio of 8.5:1.

The test in the U-CARE program suggested our global model [φ(s*t) p(s*t)] fit the data well (χ^2_{46} = 21.03, P = 0.99). The tests for the assumptions of equal catchability and homogeneous survival did not provide evidence of sampling problems such as trap dependence or presence of transients for males (test 2CT χ^2 = 10.27, df = 13, P = 0.67; test 2CL χ^2 = 6.61; df = 15; P = 0.97; test 3SR χ^2 = 3.58, df = 13, P = 0.99; test 3SM χ^2 = 0.58, df = 5, P = 0.99). The tests could not be performed in females because of the small sample size.

Starting from the global model, subsequent models with fewer parameters were built constraining the effects of sex (s) and time (t) variation. Just the three best models of this preliminary set [φ(s) p(s); φ(.) p(s); φ(s) p(.)] had W_{AIC_C} > 0.01 at the end of the analysis (Table 1). All the other preliminary candidate models with support <0.01 are not shown. The best of these models [φ(s) p(.)] indicates that variation in apparent survival (φ) could be explained by the difference between the sexes (s), so we set survival varying between sexes [φ(s)] and tested different models for recapture rates accounting for the effect of temperature, rainfall, and seasonality (Table 1). The best model explaining the variation in recapture probabilities accounted for an effect of season [p(wet/dry)] (four first models in Table 1). The recapture probability after model averaging was 0.1 ± 0.02 for males and 0.1 ± 0.03 for females in the wet season and 0.05 ± 0.02 for males and females in the dry season.

After setting recapture probability as [p(wet/dry)], we tested hypotheses of variation in survival, explained by sex (s),

rainfall (rain), temperature (temp), or no variation (.). Because sex and rainfall were the best predictors of survival, we also set models for the additive effect of these two variables [φ(s+rain) p(wet/dry)] and the interaction between them [φ(s*rain) p(wet/dry)]. The model with the additive effect of sex and rainfall was the best model for survival variation with the lower AICc value and a support of 53% (W_{AIC_C} = 0.53) (Table 1). Therefore, survival estimates in both sexes were different in *H. albopunctatus*, with males always showing higher apparent survival (ranging from 0.65 to 0.96) than females (ranging from 0.23 to 0.69) in all months (Fig. 1). And both sexes were equally negatively associated with the average monthly rainfall (β = −0.26), meaning lower survival in months with more rain.

Sexual Dimorphism.—We measured and dissected 182 individual museum specimens of *H. albupunctatus*, 151 males and 31 females. The SVL varied from a male with a 26.8-mm SVL to a female with a 63.9-mm SVL. The smallest reproductive male was 41.9 mm and the smallest reproductive female was 44.5 mm. There was a significant sex difference in body shape variables (MANOVA: Wilk's λ= 0. 013, P < 0.001) and body size (ANOVA: $F_{1,180}$ = 15.603, P < 0.001), with females larger than males. Head width and head length were the most important factors according to the discriminant analysis, with females having wider ($F_{1,180}$ = 5.526, P < 0.0001) and more elongated heads ($F_{1,180}$ = 6.468, P < 0.0001) than males.

Reproduction.—Fifteen of the 31 females dissected were reproductive, with 14 bearing eggs. The eggs had a dark pigmented animal pole and yellow vegetative pole. Mean clutch size was 899 ± 304 eggs, mean clutch volume was 2.14 ± 0.99 mm³, and the mean egg volume was 0.019 ± 0.011 mm³.

There was no correlation between female SVL and clutch size (r = 0.242, P = 0.404). Nevertheless, we found a significant correlation between female SVL and clutch volume (r = 0.567, P = 0.035) and a marginally nonsignificant correlation between female SVL and mean egg volume (r = 0.518, P = 0.058). Egg
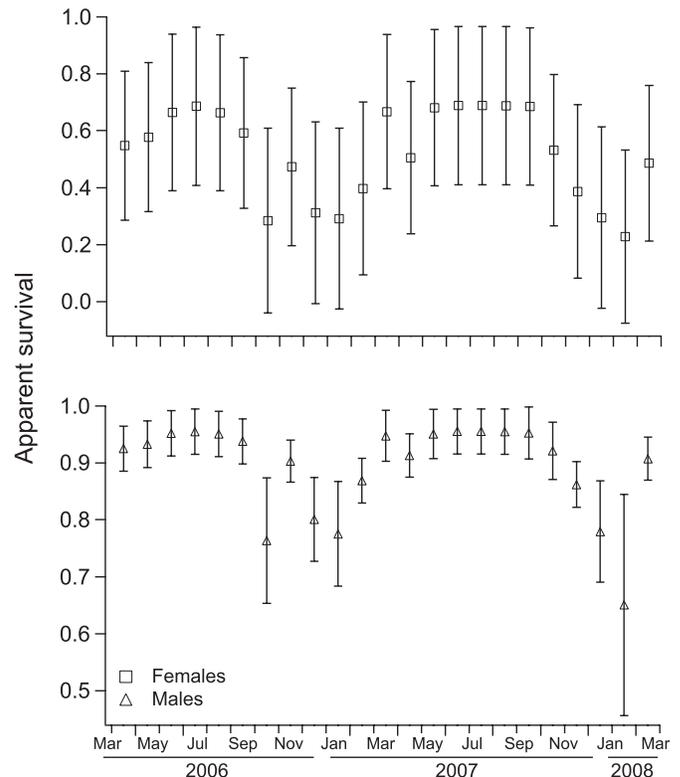

FIG. 1. Apparent survival estimates (φ) and ± SE of males and females of *Hypsiboas albopunctatus* from March 2006 to February 2008.

TABLE 2. Diet composition of *Hypsiboas albopunctatus* (N = 103). F = number of stomachs containing each prey item. Data are expressed as means ± SD.

Prey category	Frequency		Individual stomachs (mean values)				Pooled stomachs			
	F	F%	N	N%	V (mm³)	V% (mm³)	N	N%	V (mm³)	V% (mm³)
Aranae	12	25.00	0.25 ± 0.44	17.08 ± 33.07	16.10 ± 44.76	17.42 ± 35.34	13	16.04	772.58	16.76
Coleoptera	17	35.41	0.35 ± 0.48	27.15 ± 40.90	35.57 ± 79.27	30.74 ± 44.50	34	41.97	1,721.62	37.35
Blattaria	3	6.25	0.08 ± 0.35	2.57 ± 10.20	3.56 ± 17.38	1.78 ± 8.73	4	4.93	170.66	3.70
Hemiptera	2	4.16	0.04 ± 0.20	3.13 ± 16.00	0.42 ± 2.93	2.08 ± 14.43	2	2.46	20.29	0.44
Orthoptera	4	8.33	0.08 ± 0.28	7.29 ± 25.24	27.70 ± 103.01	7.59 ± 25.84	4	4.93	1,329.58	28.84
Isoptera	1	2.08	0.02 ± 0.14	2.08 ± 14.43	0.04 ± 0.029	2.08 ± 14.43	1	1.23	2.03	0.04
Odonata	1	2.08	0.02 ± 0.14	2.08 ± 14.43	2.74 ± 19.01	2.08 ± 14.43	1	1.23	131.7	2.86
Insect larvae	2	4.16	0.04 ± 0.20	2.78 ± 15.12	1.96 ± 13.23	2.11 ± 14.43	2	2.46	94.22	2.04
Nonidentified	6	12.50	0.13 ± 0.33	9.79 ± 28.55	1.45 ± 5.52	8.39 ± 27.92	6	7.4	69.42	1.51
Plant material	14	29.16	0.29 ± 0.46	26.24 ± 42.51	6.21 ± 13.33	25.72 ± 43.19	14	17.28	297.89	6.46

diameter varied between 0.53 and 2.27 mm ($\bar{x}$ = 1.69 ± 0.38 mm).

Diet Composition.—We examined 103 stomachs, but 66 of them were empty (64.1%). Nine prey categories were identified. Coleoptera (35.4%) was the most frequent prey type, followed by Aranae (25%) (Table 2). Plant material was found in 29.2% of stomachs. The most numerically important prey categories were Coleoptera, plant material, and Aranae, and the most volumetrically important prey categories were Coleoptera, Orthoptera, and Aranae, both for individual (mean values) and pooled stomachs (total values). Considering importance index (N and V together) based on individual and pooled stomachs, the most important prey categories were then Coleoptera, Aranae, plant material, and Orthoptera (Fig. 2).

Prey size and anuran head measurements were significantly correlated. The first and second canonical variables for head measurements were a contrast between head length and width, with more emphasis on head length. The first canonical variable for prey measurements was a contrast between maximum prey length and maximum prey width, with more emphasis on length (Table 3). Treefrogs with longer heads consumed longer prey items. The first canonical correlation was 0.43 and significant (Wilk's λ = 0.80, P = 0.04). The analysis indicated that the canonical variables for head measurements were good predictors of prey measurements, with 100% of variance in the latter being explained by the former (Table 3).

Discussion

Habitat and Microhabitat Use.—The present study confirms the trend for *H. albopunctatus* using mainly low bushes (e.g., Brasileiro et al., 2005; Grandinetti and Jacobi, 2005; Melo et al., 2007). Because of its widespread distribution, generalist habits, and climatic tolerance, different patterns may be seen in other localities, even within the same biome. For example, Araujo et al. (2007) found *H. albopunctatus* using the ground as the main microhabitat category in another Cerrado locality. Although this species is often considered shrub-dwelling and arboreal (Brasileiro et al., 2005), confirming its generalist habits, its occurrence in gallery forests is classified as accidental by Brandão and Araújo (2001). As expected, because our study area was essentially open, with trees occurring mainly in a gallery forest, this species was rarely found in arboreal microhabitats.

Demographic Analysis.—Males called over the 24 months of study, in agreement with the extended reproductive pattern for this species (Muniz et al., 2008). Barreto and Moreira (1996) also demonstrated continuous reproduction for this species with larval recruitment occurring throughout the year. Continuous reproduction is unusual compared with other Cerrado species

that breed during the rainy season (Bastos, 2007). Although presenting extended activity in both seasons, recapture estimates were higher in the rainy season, showing that even for a continuous breeding species in Cerrado, there might be a peak of activity and reproduction in the rainy season. Recapture rates were low, and might result from the small body size of the individuals and the microhabitat preference for bushes obstructing the view of the searcher.

Apparent survival was different for males and females of *H. albopunctatus* and negatively correlated with average daily rainfall in each month. There is no clear explanation for the negative relationship between survival and precipitation. However, the combination of increased activity of this species in the rainy season and the increased abundance or activity of anuran predators, such as water snakes, on rainy days (Scartozzoni, 2009) are probably related factors. Water snakes, such as species of the genus *Helicops*, are major predators of anurans in the Cerrado region, showing higher activity and reproductive cycle associated with precipitation (Scartozzoni, 2009). Furthermore, the lower apparent survival of females was reported for other anuran species, such as *Bufo bufo* (Fretey et al., 2004) and *Hemisus marmoratus* (Grafe et al., 2004), and was associated with their lower fidelity to the breeding site compared with males. Because the CJS model does not distinguish permanent emigration from mortality, females
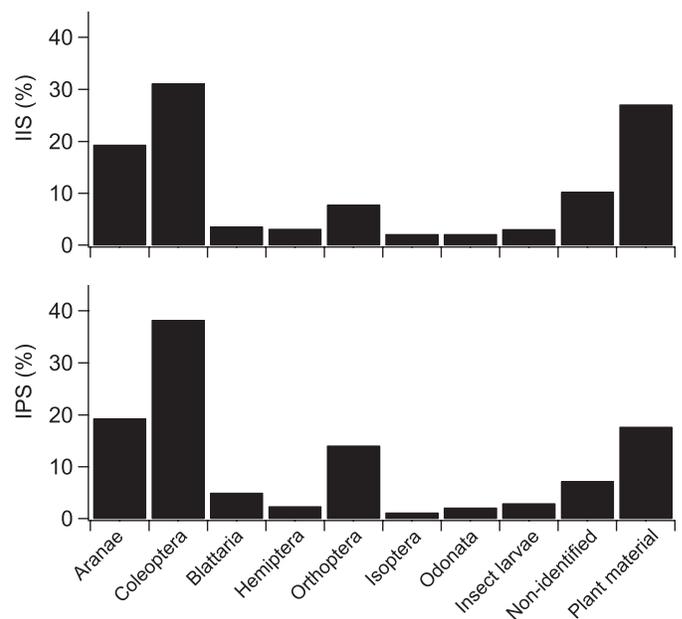

FIG. 2. Importance index based on individual stomachs (IIS) and on pooled stomachs (IPS) of prey categories ingested by *Hypsiboas albopunctatus*.

TABLE 3. Canonical correlation analysis of prey measurements vs. head measurements of *Hypsiboas albopunctatus*.

Standardized canonical coefficients for the head measurements		
	First canonical variable	Second canonical variable
Head length	1.3836	1.3288
Head width	−0.4880	−1.8552
Standardized canonical coefficients for the prey measurements		
	First canonical variable	Second canonical variable
Maximum prey length	1.2795	0.1818
Maximum prey width	−0.9511	0.8749

Canonical variables	Canonical correlation	Adjusted canonical correlation	F (approx.)	P
I	0.434	0.395	0.118	0.188
II	0.112		0.144	0.012

Wilk's $\lambda = 0.80$, $P = 0.04$ (Rejection H_0: all canonical correlations are zero)

Standardized variance of prey measurements explained by canonical variables of head measurements		
Canonical variable	Proportion	Cumulative proportion
I	0.95	0.95
II	0.05	1.00

could show a lower apparent survival rate due to increased permanent emigration from the studied pond. However, the sex differences in survival rates also could be legitimate, and this, added to the expectedly higher fidelity of males to the breeding pond (Sinsch, 1992), also could explain the biased sex ratio toward males observed in this population.

Anuran populations tend to fluctuate (Alford and Richards, 1999), especially influenced by climatic factors (Vitt and Caldwell, 2008). However, only a few studies have showed the influence of weather and adult survival. Temperature is one of the main factors affecting survival in temperate frogs; for example, several populations of the boreal toad in Colorado had lower annual survival in years with lower winter temperatures (Scherer et al., 2008), and two ranid species showed lower probability of overwinter survival in years with extremely low and variable winter temperatures (Anholt et al., 2003). Rainfall, in contrast, seems to have stronger effects on tropical species, especially the species living in seasonal habitats, such as the African frog *Hemisus marmoratus* that shows lower survival associated with arid drier years (Grafe et al., 2004). Rainfall also strongly influences survival of *H. albopunctatus* but in an opposite direction, with higher survival associated with the driest months. Because this species shows continuous activity over the year, the aridity of the driest months may not play an important role reducing survival due to physiological constraints. However, the higher abundance of predators or other factors related to increased rainfall seem to affect its survival more. The role of predator abundance and activity in the survival of this species needs to be addressed in more detail in future studies.

Sexual Dimorphism.—According to Shine (1979), females are significantly larger than males in 90% of the anuran species. This pattern also occurs in *H. albopunctatus*, which shows sexual dimorphism in body size and shape. Sexual size dimorphism in amphibians may be a result of the combined effect of relative age at sexual maturity for both sexes and growth rate (Halliday and Verrell, 1988). Because in most frog species males reach the age of sexual maturity 1 or 2 years before females (Halliday and Verrell, 1988), such difference in size can be explained by delayed sexual maturity in females.

Ultimately, reproductive costs may best explain such sexual size dimorphism. Woolbright (1989) suggests that males are smaller than females because of the higher energetic costs of male precopulatory behaviors that restrict growth. In addition, larger females can afford a greater energetic investment in egg production, increasing reproductive output by producing more and larger eggs (Kuramoto, 1978; Kaplan, 1980). Larger females

also have a higher probability of spawning twice in the same season or reproductive period (Telford and Dyson, 1990), increasing reproductive output. Furthermore, the sexual dimorphism found in *H. albopunctatus* was strong for head size (width and length). Because this is related to differences on prey sizes consumed by each sex, this dimorphism also could be the result of selection for reduced competition between the sexes (Van Sluys et al., 2001; Mesquita et al., 2004).

Reproduction.—Growth in anurans is continuous even after sexual maturity. Larger individuals in a population are usually older and present higher reproductive success (Fairbairn, 1997). Larger females of *H. albopunctatus* revealed higher reproductive output compared with smaller females, with larger clutch volume. The lack of correlation between female size and number of eggs, and mean egg volume was not expected. However, the regression results between mean egg volume and female size were close to significant. It is possible that, despite all the museum individuals dissected, the number of females sampled was not extensive enough, due to the biased sex ratio and difficulty of finding females in the field, as illustrated by our field sampling. Telford and Dyson (1990) proposed that larger females have higher chances to produce more than one clutch per season or reproductive period. Possibly, larger *H. albopunctatus* females produce more than one clutch with fewer eggs rather than producing only one clutch per year. Although we could not test the hypothesis of multiple clutches in the same breeding season, this could be the case for this species due to the extended and almost continuous reproductive season. The positive relationship between female size and clutch volume found in this study also suggests that this higher reproductive output of larger females can favor the maintenance of sexual size dimorphism in this species.

Diet Composition.—Our study suggests the diet of *H. albopunctatus* should be categorized as generalist, with Coleoptera, Aranae, and Orthoptera being the most important prey items consumed. Araujo et al. (2007) reported consumption of few larger prey items by a population of *H. albopunctatus* in another Cerrado locality, corroborating the high volumetric importance of Orthoptera and Coleoptera found in the present study. However, Araujo et al. (2007) also reported Hymenoptera and Lepidoptera as numerically abundant categories in the diet of *H. albopunctatus*. The divergence from our results probably reflects the great spatial and temporal differences among Cerrado localities, season in prey availability, or a combination of both. Seasonal variation may influence anuran diets, which could be related with both prey availability and

distinct environmental conditions (Manyero et al., 2004). Geographical and temporal variation should be considered for a complete understanding of the ecology of a species.

Prey and anuran head measurements were significantly correlated. This relationship is often related to optimal foraging (Werner and Hall, 1974), resource partitioning between sexes (Van Sluys et al., 2001), and ontogenetic changes in diet related with prey size (Manyero et al., 2004). Therefore, larger individuals can choose larger prey and avoid intraspecific competition.

Conclusions.—We conclude that the treefrog *H. albopunctatus* can be considered a generalist in both habitat and diet. Vocalization occurs throughout the year, suggesting continuous activity and reproduction, with a peak in the rainy season evidenced by the influence of seasonality on recapture rate. The higher apparent survival rates for males can contribute to the biased sex ratio toward males, with rainfall being negatively associated with survival in both sexes. In addition, the sexual size dimorphism can be the result of the selective pressure for larger females favored by the positive relationship between female size and clutch volume, the reduced competition for diet with males having shorter heads, or both. In summary, demographic patterns, reproduction, and diet are essential components to understand the ecology of a species, especially in tropical areas with high diversity and negligible knowledge about abundant species.

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