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Calling Behavior and Parasite Intensity in Treefrogs, *Hypsiboas prasinus*

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ABSTRACT.—**A negative relationship between parasite intensity and male ornament condition or sexual display rate is one of the conditions of the parasite-mediated sexual selection model. In anurans, temporal properties of calling behavior, and particularly calling rates, are the best candidates to express a negative relationship with parasite intensity, given the high energy costs of calling and the fact that calls are potentially under strong intersexual selection. We studied the relationship between call parameters and helminth parasite intensity in males of a Brazilian subtropical treefrog, *Hypsiboas prasinus*. We tested the hypotheses that: 1) calling characteristics are correlated negatively to parasite intensity; and 2) the relationship between calling performance and parasite intensity is more pronounced when dynamic properties are considered. According to our predictions, only rate, the most important dynamic property of calling behavior, is associated with individual variation in parasite intensity. Males that call at higher rates show lower total parasite intensity. The negative relationship between parasite intensity and calling rate in *H. prasinus* could be because of the higher energy cycles associated with the maintenance of high calling performance. Also, theoretically, calling rate could work as an honest signal of anuran male quality, although the causal relationship between calling variation and parasite intensity, as well as the relevance of this relationship for female choice and male reproductive success, remain to be investigated.**

The evolution of traits sexually selected by female mate choice present a fascinating evolutionary paradox, especially when males do not provide a direct benefit to the female or their offspring (Anderson, 1994). One solution to this puzzle predicts that females should exercise mate choice based on condition-dependent traits that evolve as honest signals of the heritable quality of males (Fisher, 1915; Zahavi, 1975). However, a theoretical difficulty for this evolutionary model, known as the "good genes" hypothesis, is that persistent directional selection is expected to deplete additive variance on fitness (Roff, 1997). Hamilton and Zuk (1982) proposed that continual change in genetic composition of parasite populations may maintain additive genetic variance in resistance, and therefore fitness, in populations of their hosts. According to Hamilton and Zuk (1982), this process could result in the selection of males with well-developed secondary sex ornaments that reflect the degree of resistance to parasitism. One of the conditions for the parasite-mediated sexual selection model to be fulfilled is that male ornament condition or sexual display rate decreases with increased parasite intensity, an assumption that has gained mixed support from studies in different phylogenetic groups (Anderson, 1994). Only two studies have been conducted on anurans and neither found a relationship between parasite infection and mating success (Hausfater et al., 1990; Tinsley, 1990). Only one of the studies measured parameters of calling behavior, the main target of intersexual selection in anurans. Hausfater et al. (1990) found no relationship between parasite intensity and measures of call performance, time of arrival of males in the chorus, or chorus attendance.

Intersexual selection in anurans is based largely on properties of male calls that were classified by Gerhardt (1991) as static or dynamic according to their coefficient of variation. While static properties such as dominant frequency display coefficients of variation generally lower than 4%, dynamic properties such as call rates are characterized by a coefficient of variation of 20% or more (Gerhardt, 1991). In general, preference by females results in stabilizing or weakly directional selection on static or spectral call properties and highly directional selection on dynamic or temporal properties (Gerhardt, 1991; Wells, 2007; Castellano et al., 2009). In natural ponds, males that produce calls that are louder, longer, and more complex or at higher rates are probably detected more easily and attract more females (e.g., Wells, 2007). However, despite increasing mating success, the maintenance of high calling effort suggests physiological tradeoffs that may be costly to males. Dynamic properties of calls, especially calling rate, in most of the species studied entail high energetic expenditure (e.g., Pough et al., 1992; Wells, 2001). Additionally, calling rates are correlated positively to plasma levels of immunosuppressive steroids (Emerson and Hess, 1996; Leary et al., 2005), increasing the probability of higher parasite intensity (Folstad and Karter, 1992; Wingfield, 1994).

Given that dynamic properties of calls could be subjected to intersexual directional selection and entail high physiological costs, they may signal the quality of males, including their genetic resistance to parasites, to females. Among dynamic properties, calling rate is particularly suited to intersexual selection. We tested the hypotheses that: 1) calling characteristics are correlated negatively to parasite intensity; and 2) the relationship between calling performance and parasite intensity is more pronounced when dynamic properties are considered. To test these hypotheses we studied the relationships between call parameters and helminth parasite intensity in males of a Brazilian subtropical tree frog, *Hypsiboas prasinus*. Because *H. prasinus* reproduce throughout the year, despite significant seasonal changes in temperature and rainfall (Haddad and Sazima, 1992; Kiss et al., 2009), and because dynamic properties of calls can be temperature sensitive (Wells et al., 1996; Navas, 1996), we investigated the relationship between calling behavior and parasite intensity during the summer and winter.

MATERIALS AND METHODS

Study Animal and Sites.—*Hypsiboas prasinus* is a treefrog occurring in the Atlantic Forest in southeastern Brazil at moderate altitudes. These frogs reproduce year round (Haddad and Sazima, 1992; Faivovich et al., 2004; Kiss et al., 2009). Males call at night, partially submerged or floating in water, or on soil

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or rocks, or perched on vegetation around the lakes. The spawn is deposited around submerged vegetation (Haddad and Sazima, 1992). Calling males were captured from a single breeding site at Recanto Sacae Watanabe, Botucatu (48°30′W, 22°59′S) in São Paulo State, Brazil. The study area is a typical semideciduous seasonal forest and has an altitude of 832 m. In this environment, summer defines a wet–warm season from October to March whereas winter is a dry–mild season from April to September (Tubelis et al., 1971). All captured specimens were males and collections were concentrated during summer (January–March 2009, $N = 17$) and winter (July–August 2009, $N = 25$). During observations chorus density varied daily from 75 to 90 males.

Behavioral Observations.—Calling males were located visually and observed for 30 min to quantify calling behavior. This period of observation was sufficient to evaluate the calling rate because males of this species call at relatively constant rates throughout the night. To reduce interference of observers on behavior we used red lamps and started to record behavior 10 min after an individual had been detected. All observations were performed during the period of maximum calling activity, between 1900 h and 2400 h. For each individual, the number of calls was counted and divided by sample time to estimate average calling rate during the observation period (number of calls per hour). Advertisement calls from individual males were recorded using a Seinnheiser (ME-67) microphone and a Marantz PMD 201 tape recorder positioned 1 m in front of the calling male. Recordings were analyzed using Raven Lite 1.0 (Cornell Laboratory of Ornithology, Interactive Sound Analysis Software). Each call of *H. prasinus* is composed of three notes (Fig. 1), and we used spectrograms to measure fundamental frequencies of notes 1, 2, and 3 and oscillograms to measure duration of at least five calls from each male. Calling rates, duration of calls, and the mean fundamental frequency of the three notes were used in the analyses. Four temperature data loggers (HOBO) were placed in the microenvironments normally used by vocal males and programmed to record data at 5-min intervals during observations.

Frog Capture and Parasite Collection, Quantification, and Identification.—The frogs were captured by hand and placed in individual plastic containers provided with water-soaked foam and artificial plants. Animals were then transported to the laboratory where they were euthanatized with sodium tiopental solution (Thiopenthax®). Mass was recorded to the nearest 0.001 g and the digestive tract, body cavity, lungs, liver, and urinary bladder of each individual were examined for helminth parasites under a stereomicroscope. Helminths were fixed, quantified, and identified to family, genus, or species (sensu Madelaire et al., 2012). Lung, small intestine, and large intestine parasite intensities correspond to *Rhabdias* cf. *fuelleborni* (nematode), *Cylindrotaenia americana* (tapeworm), and nonidentified Cosmocerciid (nematode) intensities, respectively. Total parasite intensity is the sum of the intensity of all parasites encountered for each host.

Data Analysis.—All variables were submitted initially to descriptive statistics and were $\log_{10}$ transformed to improve normality prior to subsequent analyses. Temperature was not correlated to variation in behavioral variables within seasons (winter, r_s range from -0.33 to 0.05, $P \geq 0.13$; summer, r_s range from -0.69 to 0.39, $P \geq 0.06$) and was not included in the tested models. The continuous dependent variables (body mass and parasite intensity) were not correlated. We tested for additive effects of body mass, total parasite intensity, and season on behavioral variables (calling rate, call duration, and call frequency) by using general linear models implemented in R software, version 2.10.0 (R Development Core Team, 2010). We also tested for an interaction between body mass and total parasite intensity, given that a positive relation between parasite biomass and host body size has been frequently described in the literature (Poulin and George-Nascimento, 2007). As different models differ in the number of parameters, we extracted the second-order Akaike information criterion (AIC_c; Akaike, 1974), which penalizes the likelihood of a given model as a function of the number of parameters and corrects for low sample sizes. The AIC_c value ($\Delta AIC_c < 2.0$) and the Akaike weight ($WAIC_c$) were used to determine which models had the most support. $WAIC_c$ describes the relative strength of the evidence in support of a particular model. The best model corresponds to the one with the lowest AIC_c value, providing a good fit to the data with the fewest parameters possible (Burnham and Anderson, 2002). To select between competing models with $\Delta AIC_c < 2.0$, we calculated the log likelihood and considered the model that presented the lower value.

RESULTS

Descriptive analyses of all variables are presented by season (Table 1). The most highly supported model for calling rates indicated a negative association with parasite intensity. Moreover, this behavioral variable was affected by the interaction between body mass and parasite intensity, indicating that the relationship between calling rate and parasite load was more pronounced in smaller males (Tables 2 and 3; Fig. 2). The second most-supported model for calling rate was 1.9 ΔAIC_c from the most-highly supported model and included season as an additional explanatory variable, but the comparatively higher log likelihood of this model and the lack of significance of season indicated that the inclusion of this parameter did not improve explanatory power (Table 3).

For call duration, the most-highly supported model indicated that this variable was affected by body mass and season, although body mass did not show a significant *P*-value in the first model (Tables 2 and 3). The second model was 1.8 ΔAIC_c from the most-highly supported model and excluded body mass, attaining a lower log-likelihood value (Tables 2 and 3).

Similarly, the model for fundamental frequency that received the strongest support included only a nonsignificant effect of season, and the second model was 0.7 ΔAIC_c from the most-highly supported model and excluded season, attaining a lower log-likelihood value (Tables 2 and 3). Therefore, variation in fundamental frequency cannot be associated with season, body mass, or parasite intensity.

DISCUSSION

According to our predictions only calling rate, a dynamic property of calling behavior, is associated with individual variation in parasite intensity. Individuals that call at higher rates are less infected by total parasites. Previous studies that tested the role of parasite-mediated sexual selection in anurans did not quantify calling behavior (Tinsley, 1990) or assessed calling for only brief periods (Hausfater et al., 1990). However, dynamic call properties present large, within-bout variation, requiring long recordings for accurate measures of interindividual variation (sensu Gerhardt, 1991). This is particularly true for measures of calling rates—mainly in species characterized by temporal organization of the chorus in defined bursts of

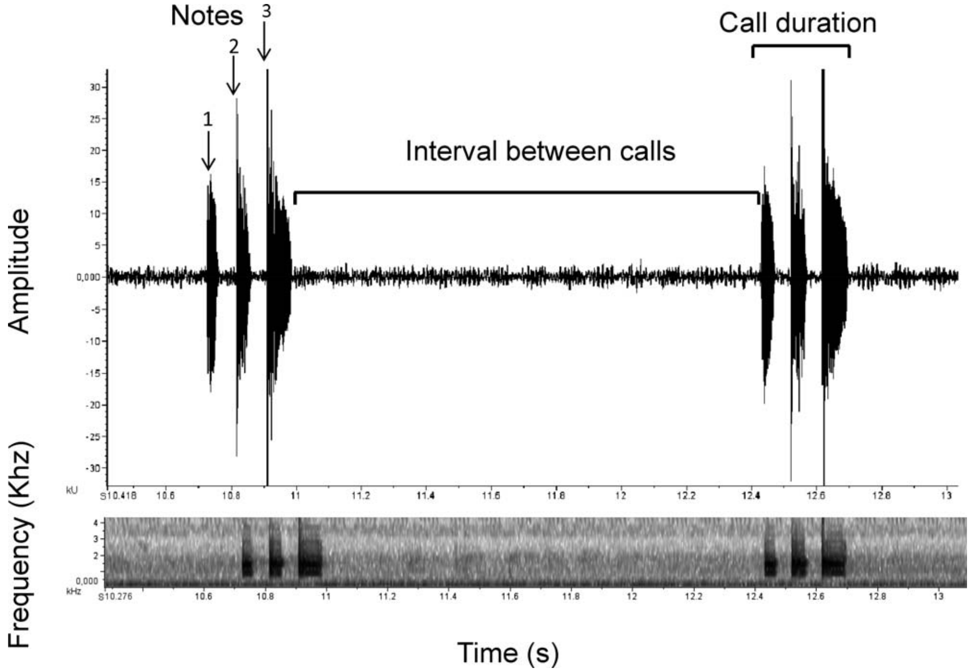

FIG. 1. Two typical calls from *Hypsiboas prasinus* consisting of three notes each. Oscillogram (top) showing changes in amplitude over time with discrimination of the call duration. Spectrogram (bottom) showing changes in frequencies over time.

calling followed by periods of silence (Schwartz, 2001; Bevier et al., 2008). Our effort to observe a large number of individuals for 30 min each may have been important in finding the relationships between parasite intensity and dynamic properties of calls in *H. prasinus*.

Parasite infection is often associated with an imbalance of energy and nutrients, as costs are increased by mounting an immune response to infection, repairing tissue damage, and replacing nutrients used by parasites (Lochmiller and Deerenberg, 2000; Tinsley et al., 2002; Kristan and Hammond, 2004). Energy input can be decreased by parasite-induced anorexia and reduced efficiency of nutrient assimilation (Holmes and Zohar, 1990; Kyriazakis et al., 1998; Kristan, 2002). The observed influence of body size on the relationship between calling rate and parasite intensity in *H. prasinus* might be related, at least in part, to the fact that parasite infection decreases growth rates in different vertebrates including toads (Goater and Ward, 1992; Kelehear et al., 2009). Although we did not estimate the age and growth rates of our study animals, if smaller individuals are younger ontogenetic changes in immunocompetence might also influence the observed relationship (Rollins-Smith, 1998). The effects of parasites on host phenotype can be dependent on infection level (Goater et al., 1993; Clobert et al., 2000; Schwanz, 2006; Møller, 2008). For example, effects may be expressed during periods of high aerobic activity or intense stress of the hosts but remain practically unnoticeable during periods of low energetic demand (Holmes and Zohar, 1990; Goater et al., 1993). Given that anuran calling is a sustained activity characterized by high energetic costs and supported mainly by aerobic metabolism (Bevier, 1995; Ressel, 1996; Carvalho et al., 2008), a relationship between parasite intensity and calling rate in *H. prasinus* is reasonable. We need also to consider that we captured adult treefrogs from the wild, at which point the host–parasite relationship (if present) had already been established and present for a variable and potentially long time. Consequently, our data do not permit the establishment of a causal relationship between physiological condition, parasite intensity, and calling performance (Beldomenico and Begon, 2010). A probable scenario is that individual variation in physiological condition and susceptibility to infection initially

TABLE 1. Seasonal descriptive analyses of operational temperature (°C), parasite load, and morphological and vocal variables of *Hypsiboas prasinus* from Botucatu, Sao Paulo, Brazil. N = number of measurements, SD = standard deviation.

	Summer			Winter		
Variables	N	Mean	SD	N	Mean	SD
Temperature	441	22.26	1.86	813	10.98	2.64
Lung parasites	17	5.88	15.18	25	1.80	2.65
Small intestine parasites	17	1.00	1.28	25	1.64	3.09
Large intestine parasites	17	0.18	0.39	25	0.28	0.84
Total parasites	17	7.06	15.61	25	3.72	4.06
Body mass (g)	17	4.07	1.11	23	4.10	1.06
Calling rate (call/h)	17	279.49	325.93	25	298.72	236.47
Calling duration (sec)	11	0.21	0.03	22	0.31	0.06
Fundamental frequency (Hz)	10	0.96	0.23	23	0.78	0.20

TABLE 2. Akaike statistics of models for calling rate, call duration, and call frequency of *Hypsiboas prasinus* considering effects of body mass, total parasite intensity (parasites), and season. Additive effects and interactions are represented by + and *, respectively. AICc = Akaike's information criterion for small samples; K = number of parameters; ΔAIC_c = difference of AICc between any model and the best model; WAICc = weight for each model.

Response variable	Model	AICc	K	ΔAIC$_c$	WAICc
Calling rate	Body mass * parasites	84.3	5	0.0	0.4664
	Body mass * parasites + season	86.2	6	1.9	0.1770
	Body mass + parasites	86.5	4	2.2	0.1523
	Body mass	87.5	3	3.2	0.0955
	Body mass + parasites + season	88.6	5	4.3	0.0538
	Body mass + season	89.0	4	4.7	0.0435
	Parasites	92.8	3	8.5	0.0068
	Parasites + season	94.9	4	10.6	0.0023
	Null	95.5	2	11.2	0.0017
	Season	97.2	3	12.9	<0.001
Call duration	Body mass + season	−69.3	4	0.0	0.5018
	Season	−67.5	3	1.8	0.2026
	Body mass + parasites + season	−67.3	5	2.0	0.1821
	Parasites + season	−65.3	4	4.0	0.0671
	Body mass * parasites + season	−64.6	6	4.8	0.0463
	Body mass	−49.1	3	20.3	<0.001
	Body mass + parasites	−47.6	4	21.7	<0.001
	Null	−46.5	2	22.9	<0.001
	Body mass * parasites	−45.9	5	23.4	<0.001
	Parasites	−44.8	3	24.6	<0.001
Call frequency	Season	−22.5	3	0.0	0.3407
	Null	−21.8	2	0.7	0.2397
	Body mass + season	−20.1	4	2.4	0.1032
	Parasites + season	−19.9	4	2.6	0.0928
	Body mass	−19.4	3	3.1	0.0711
	Parasites	−19.4	3	3.2	0.0703
	Body mass * parasites + season	−17.5	6	5.0	0.0277
	Body mass + parasites + season	−17.4	5	5.2	0.0255
	Body mass + parasites	−16.8	4	5.8	0.0189
	Body mass * parasites	−15.5	5	7.1	0.0099

determine differential parasite intensity, and this variation in parasite intensity further alters physiology and behavior of hosts in an ongoing process.

Calling performance in ectotherms is expected to decrease at lower temperatures (Prestwich, 1994), although males from anuran species characterized by low calling rates might be less sensitive to temperature (Navas, 1996). Despite seasonal differences in mean temperature of about 11°C in Botucatu, the only call property from *H. prasinus* that showed a consistent effect of season was call duration, with individuals displaying

TABLE 3. Parameter estimate, standard error (SE), *P*-value, and log likelihood from models with $\Delta AIC_c \leq 2.0$. Asterisks indicate the interaction between body mass and parasites.

	Parameters	Estimate	SE	*P*	Log likelihood
Calling rate					
Model 1	Intercept	3.313	1.323	0.0169	−36.265
	Body mass	−1.195	2.030	0.5598	
	Parasites	−4.400	1.841	0.0222	
	Body mass*parasites	6.121	2.838	0.0378	
Model 2	Intercept	3.241	1.330	0.020	−35.844
	Body mass	−1.263	2.039	0.539	
	Parasites	−4.463	1.849	0.021	
	Season	0.177	0.205	0.393	
	Body mass*parasites	6.265	2.853	0.034	
Call duration					
Model 1	Intercept	−0.366	0.073	0.000	39.245
	Body mass	−0.244	0.119	0.051	
	Season	−0.152	0.028	0.000	
Model 2	Intercept	−0.674	0.023	0.000	37.100
	Season	0.162	0.029	0.000	
Model 3	Intercept	−0.499	0.082	0.000	39.543
	Body mass	−0.253	0.122	0.046	
	Parasites	−0.023	0.032	0.470	
	Season	0.149	0.028	0.000	
Fundamental frequency					
Model 1	Intercept	−0.129	0.035	0.001	
	Season	0.103	0.058	0.088	14.711
Model 2	Intercept	−0.093	0.0289	0.003	13.129

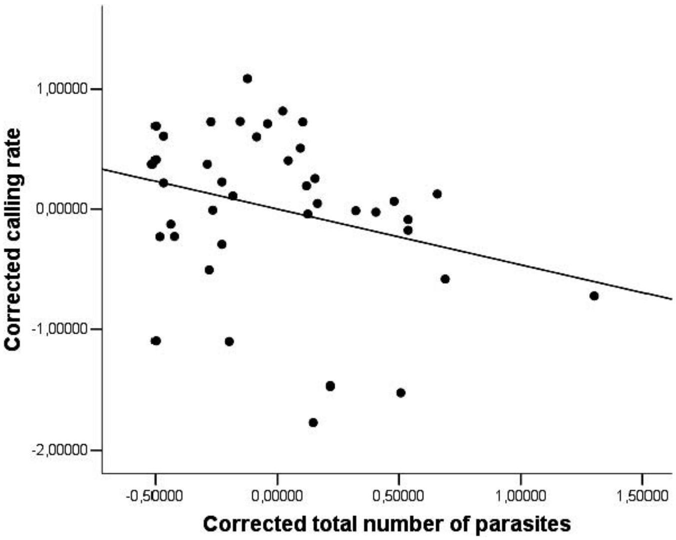

FIG. 2. Partial plots of the calling rate versus total number of parasites of *Hypsiboas prasinus*. Corrected calling rate and total number of parasites are the residuals of a regression of body mass. The line is illustrative.

longer calls during winter. Although these longer calls during winter might be interpreted as an effect of seasonal differences in temperature (O'Neill and Beard, 2011), both static and dynamic call properties were not related to temperature variation within seasons. Our data corroborate previous observations by Kiss et al. (2009) from another population of *H. prasinus* that calling rates do not change between seasons and suggest that variation in calling rates among individuals of this species result more from modulation by social interactions than from differences in physiological limitation by temperature, even during winter.

Several field studies have emphasized the importance of male rivalry on anuran sexual selection, which produces variation in chorus attendance and, by consequence, affects the cumulative probability of mating (Gerhardt and Huber, 2002; Friedl and Klump, 2005). However, recent evidence points to relatively strong directional selection on call rate in treefrogs (Castellano et al., 2009). Our results show that calling rate is inversely related to parasite load in *H. prasinus*. In this way, theoretically, calling rate could work as an honest signal of anuran male quality, although the causal relationship between calling variation and parasite intensity, as well as the relevance of this relationship to female choice and male reproductive success, remains to be tested.

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