Herpetological Review, 2004, 35(3), 239–243.

Vocalizations and Aggressive Behavior of *Phyllomedusa rohdei* (Anura: Hylidae)

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The complexity of anuran reproductive behavior in prolonged breeders has been described in several neotropical species (Bastos and Haddad 1995, 2002; Martins et al. 1998; Pombal et al. 1994). For example, in contrast to explosive breeders, prolonged breeders often have a variety of functionally different vocalizations that are used during the breeding seasons (Bastos and Haddad 1995, 2002; Cardoso and Haddad 1984; Martins and Haddad 1988). Thus, besides advertisement and release calls, some prolonged breeders frequently also emit courtship, encounter, reciprocal, and territorial calls (Bastos and Haddad 2002; Given 1987; Martins and Haddad 1988).

The main reason males compete with each other in breeding aggregations is the scarcity of females (Wells 1977). Males that engage in agonistic interactions sometimes assess the fighting ability of potential opponents, possibly to avoid physical encounters with larger, stronger rivals. One way to do this is to escalate from non-physical to physical interactions, relaying information about body size or motivation before necessarily becoming involved in costly combat. Thus, non-physical displays (e.g., vocal interactions) might be able to resolve conflicts before escalating to physical combat when interacting males differ greatly in size, allowing smaller males to avoid physical encounters with larger opponents (Given 1988; Howard 1978; Parker 1974). Generally, three characteristics determine the outcome of fights: (1) size (Davies and Halliday 1978; Dyson and Passmore 1992; Howard

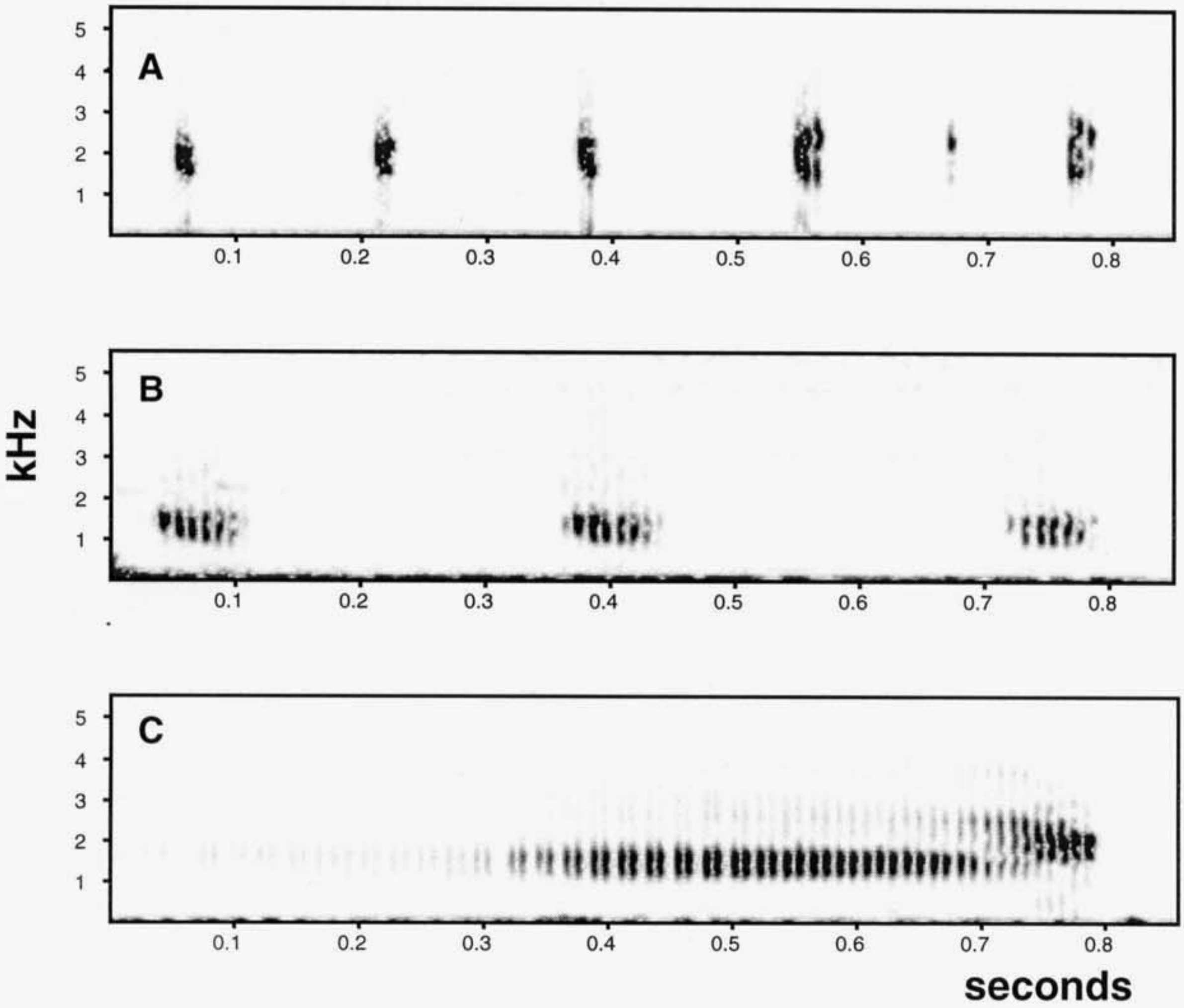

FIG. 1. Sonograms of vocalizations of *Phyllomedusa rohdei*: (A) advertisement call with extra note between the last two notes; (B) territorial call type 1 (T1); (C) territorial call type 2 (T2).

1978), (2) residence (Crump 1988; Given 1988; Pombal et al. 1994), and (3) body condition (Bastos and Haddad 2002).

Our main aim in this paper is to examine the vocal repertoire and aggressive behavior between males of *Phyllomedusa rohdei* Mertens, 1926. Our objectives were to: (1) describe the different call types, (2) describe the social context in which each call type was emitted, (3) describe behavior during aggressive encounters, and (4) determine whether size, residence, or body condition influenced the outcomes of fights.

We studied *P. rohdei* in a temporary pond approximately 170 m^2, located at the edge of a forest at Palmital (22°50'S; 42°27'W), Municipality of Saquarema, State of Rio de Janeiro, southeastern Brazil. The population was monitored from July 1999 to July 2000 for a total of 84 nights (411 h). The visits were monthly when the pond was dry (from July 1999 to November 1999 and from March 2000 to July 2000), and every two weeks when the pond held water (from December 1999 to February 2000). Field observations were conducted usually between 1700 h and 24 h.

Snout–vent length (SVL) was measured to the nearest 0.1 mm with calipers and body mass weighed to the nearest 0.05 g with a Pesola® balance. Individuals were weighed weekly or more frequently when they engaged in aggressive interactions. Males were marked individually by toe clipping (opposable fingers and toes were not clipped).

Focal animal and all occurrence sampling were used for behavioral records (Lehner 1979). A winner was the male that remained in a site after an encounter, while the loser was the one that moved away from the site where the fight occurred. A male was considered a resident if he was the first male to occupy a determined site or if he was already calling or patrolling (see Matos et al. 2000) at the beginning of the focal observations. The time of residence of males was the total number of nights a male spent in a same site.

We recorded the vocalizations with UHER 4000 recorder at a tape speed of 19 cm/s and UHER microphone. Calls were analyzed by the software Avisoft-Sonograph Light 1, version 2.7. The nomenclature of vocalizations follows Duellman and Trueb (1994).

For statistical analysis of results, we used Student's t-test, ANOVA, and Spearman's correlation coefficient (r_s) (Zar 1999). Body condition was estimated by a regression between logs of SVL and mass. We compared slopes of SVL versus mass regressions between winners and losers of aggressive encounters (Zar 1999). Descriptive statistics are given as mean ± SD.

Phyllomedusa rohdei males used vocalizations and physical interactions to defend calling sites. The vocal repertoire included

TABLE 1. Summary of acoustical parameters of the vocalizations of *Phyllomedusa rohdei*. Values are presented as mean ± SD (range) (N).

Characteristics	Calls Types Advertisement	 Territorial 1	 Territorial 2
Call duration (ms)	553.0 ± 201.0 (178.0–1123.0) (63)	1152.0 ± 718.0 (345.0–3626.0) (18)	841.0 ± 209.0 (574.0–1178.0) (16)
Number of notes	4.3 ± 1.4 (2–7) (63)	4.7 ± 2.4 (2–13) (18)	1
Note duration (ms)	18.0 ± 5.0 (7.0–34.0) (270)	70.0 ± 12.0 (44.0–95.0) (75)	—
Interval between notes (s)	144.0 ± 29.0 (25.0–223.0) (208)	223.0 ± 38.0 (155.0–323.0) (58)	—
Number of pulses	2.3 ± 0.5 (1.0–4.0) (245)	7.8 ± 1.0 (4.0–10.0) (70)	71.2 ± 22.2 (44.0–116.0) (9)
Pulse durations (ms)	7.0 ± 2.0 (3.0–14.0) (549)	6.0 ± 2.0 (3.0–13.0) (420)	7.0 ± 2.0 (3.0–13.0) (303)
Dominant frequency range (kHz)	1.3 ± 0.1 to 2.6 ± 0.2 (1.1–3.2) (62)	0.8 ± 0.1 to 1.9 ± 0.3 (0.7–2.6) (18)	1.2 ± 0.3 to 2.5 ± 0.3 (0.9–3.0) (16)

six types of vocalizations: advertisement call, two territorial calls, two encounter calls, and one release call.

The advertisement call (Fig. 1A, Table 1) was the most common call emitted in breeding aggregations. Males emitted this call at irregular intervals throughout the night. Each call had 1–7 multipulsed notes. One-note calls were emitted frequently at the beginning of the night or in choruses of one or two calling males. Calls greater than three notes sometimes had an extra note of lower intensity between the last two notes (Fig. 1A). In close-range vocal interactions between males of *P. rohdei*, several advertisement calls were emitted in response to another advertisement call or to territorial ones, even when the behavior of both opponents increased in aggressiveness.

Males emitted territorial calls either in response to the advertisement or territorial calls of neighboring males (isolated males did not emit these vocalizations). We observed two types of territorial calls: type 1 (T1) is composed of 2–13 short multipulsed notes (Fig. 1B, Table 1) and type 2 (T2) is a long multipulsed note (Fig. 1C, Table 1). In several agonistic interactions the T1 call was emitted frequently before the T2 by the same male, suggesting an escalated aggressive behavior.

In a few cases, we observed two unusual sounds that were added

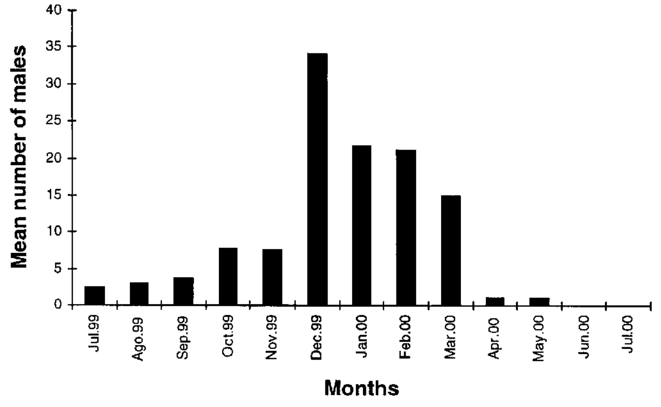

FIG. 2. Mean number of calling males of *Phyllomedusa rohdei* during study period.

TABLE 2. Size difference and resident status of winners of aggressive encounters where opponent differed by more than 3.0 mm in SVL. A positive size difference means that the winner was larger than the loser.

Resident Status	Size difference (mm)
I	9.7
I	7.0
R	6.1
R	4.8
I	4.0
R	3.0
R	-3.3
R	-4.0
R	-4.2
R	-4.4

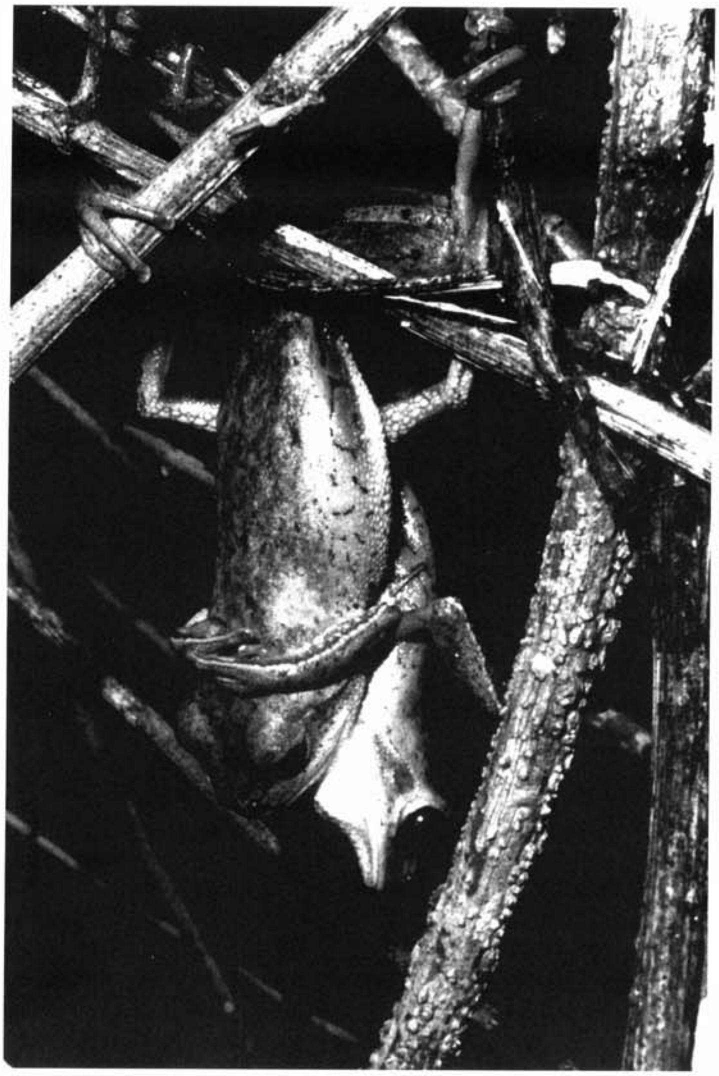

FIG. 3. Two males of *Phyllomedusa rohdei* in physical combat.

at the end of the territorial calls. Both types consisted of multipulsed notes emitted by resident males during close-range agonistic interactions. Judging by the social context within which they were evoked, these unusual sounds are probably encounter calls.

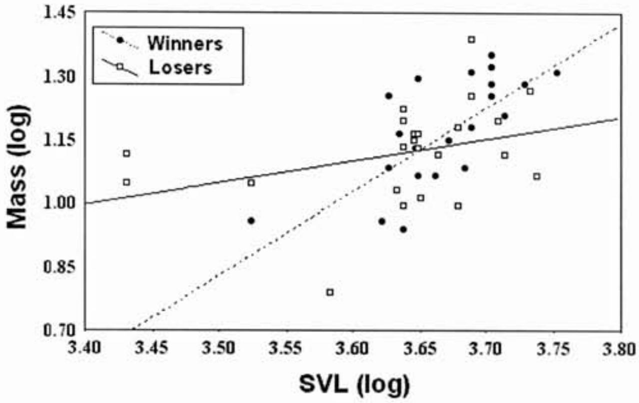

FIG. 4. Linear regression between SVL and mass of winners and losers of aggressive encounters. Variables were log-transformed prior to the analysis.

Finally, a male emitted release calls when trying to dislodge an opponent from his back. These calls are similar to the T1 call with lower intensity.

When neighboring males approached each other and emitted advertisement calls, antiphonal calling between rivals took place. Calls escalated from advertisement calls to both types of territorial calls. One or both males walked under the vegetation searching for the other. Sometimes an individual ceased searching and remained silent or resumed advertisement calling, apparently tolerating its neighbor. However, when males met, vocal interactions continued with two alternative outcomes: (1) one male fled while the other pursued with no fighting, or (2) physical combat occurred. In 15 pursuits observed, the pursuer male was larger (mean ± SD, 39.7 ± 2.1 mm) than the pursued (38.1 ± 1.9 mm; t = 2.20; P = 0.03). However, pursuer and pursued males were not significantly larger (38.9 ± 2.1 mm; N = 30; t = 0.15; P = 0.88) than males that actually fought (38.8 ± 2.5 mm; N = 54). Likewise, the body size differences of males involved in pursuit (2.16 ± 1.93 mm; N = 15) versus those involved in fights (2.65 ± 2.33 mm; N = 27) also were not significantly different (t = -0.69; P = 0.49). Only four pursuer males (27.7%) were smaller than pursued ones. The body differences for all 15 pursuer/pursued pairs were significantly different than zero (F = 18.70; P = 0.0002).

When the pond was dry, we observed only male-male vocal interactions and no physical combat. The distances between calling males before Dec / 99 (pond dry) were larger (154.17 ± 86.40 cm; N = 18) than distances between males after Dec / 99 (pond full) (55.00 ± 37.99 cm; N = 23; t = 4.78; P = 0.00002). More calling males were present when the pond was full than when it was dry (Fig. 2).

During physical combat, each male tried to seize the opponent with his arms and feet (Fig. 3). The uppermost male seized his opponent by the head, neck, or waist, and shook him up and down. The fight finished when the seized male was released by the other or escaped. The loser quickly left and remained in a submissive posture or called from a farther distance than before the interaction, while the winner returned to the original site and resumed calling. Sometimes, winner males oriented toward the loser and shook his body up and down. The duration of fights ranged from 10 s to 30 min and each male had an average of 1.5 fights (range 1–6; N = 36) over the entire breeding season.

In 27 aggressive encounters, the winners (SVL = 39.2 ± 2.1 mm; N = 27; mass = 3.21 ± 0.42 g; N = 23) were not significantly larger (t = 1.23; P = 0.23) nor heavier (t = 1.05; P = 0.30) than losers (SVL = 38.4 ± 2.8; N = 27; mass = 3.08 ± 0.36; N = 23), but the slope of the SVL versus mass regression of winners was significantly higher (b = 1.983 ± 0.43; F = 7.07; P = 0.01) than that of losers (b = 0.519 ± 0.31), indicating that the winners were in better body condition than losers (Fig. 4). When resident and intruder status was determined, 18 of 25 (72%) winners of fights were residents males. The mean time (± SE) of residence of males that fought was 2.2 ± 1.9 nights (range = 1–8; N = 48). Ten fights occurred between males with differences greater than 3.0 mm (Table 2). Smaller males only won these fights when they were residents.

The complexity of the vocal repertoire in *P. rohdei* reflects social behavior typical of a prolonged breeder (Bastos and Haddad

2002; Cardoso and Haddad 1984; Wells 1977). A secondary function for many vocalization types can be associated with male-male evaluation, especially when aggressive behavior takes place. Threat signals sometimes evolve to enable contestants to assess each other's strength or motivation without resorting to a serious fight (Andersson 1980; Davies and Halliday 1978; Wells 1978). Besides the use of advertisement call, males of *P. rohdei* have two distinct territorial calls and probably two encounter calls. Variable aggressive calls may represent a graded communication system, because these calls may signal the motivational state of the combatants (Given 1987; Martins et al. 1998). In *P. rohdei*, males may be able to assess opponents through acoustic displays, because pursuer males were larger than those pursued and the SVLs of males involved in fights were not different. In other words, if your rival is bigger, run away, and if he is of similar body size, confront him. Nevertheless, differences in size between males engaged in fights (winner/loser pairs) versus pursuer/pursued pairs were not significantly different.

We did not observe physical combat when the pond was dry. This probably can be explained by the greater distance between males when the pond was dry (a mean of 155 cm versus 55 cm when the pond was filled), resulting in fewer close-range male-male encounters. As observed by Sullivan and Hinshaw (1992), low population density was responsible for an apparent lack of direct male-male competition for mates during breeding aggregations of *Hyla versicolor*. When males of *Phyllomedusa hypochondrialis* were distant from each other, fights were not observed (Matos et al. 2000).

In some cases, winners performed visual displays toward losers during aggressive encounters. This behavior was similar to "body jerking" defined by Hödl and Amézquita (2001). However, in body jerking, the movements were performed forward and backward instead of up and down.

Our results showed that residence and body condition influenced the results of 27 aggressive encounters between males of *P. rohdei*. A resident male in better physical condition might have better fighting ability because of larger energy reserves, higher motivational state, or different hormone levels (Wells 1978). Small males only won fights if they were the resident.

Acknowledgments.—We thank Clarissa Canedo, Márcio Martins, Mac F. Given, and Martha L. Crump for their critical reading of and suggestions for the manuscript. We thank F. N. Ramos for field assistance. We are grateful to the CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico), FAPERJ (Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro), and FUJB (Fundação Universitária José Bonifácio) for financial support.

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