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TERRITORIAL ENCOUNTERS AND THREAT DISPLAYS IN THE NEOTROPICAL FROG *PHYLLOMEDUSA SAUVAGII* (ANURA: HYLIDAE)

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The hylid frog *Phyllomedusa sauvagii* (Fig. 1) is found primarily in the Chacoan regions of eastern Bolivia, northern Paraguay, Mato Grosso do Sul in Brazil, and northern Argentina (Frost 1985). These frogs are strictly arboreal and adults average 67–75 mm SVL (Perotti 1995). Behaviors associated with reproduction have been well documented in *P. sauvagii* (e.g., Agar 1910; Cei 1980; Lavilla and Scrocchi 1988; Perotti 1995). At night, males ascend trees, position themselves near or on branches overhanging water, and call. Once in amplexus, pairs form nests using their hind legs to surround their eggs with leaves from vegetation overhanging pools of water. At the time of hatching, the larvae fall into the water where they continue their development to metamorphosis. When calling sites over bodies of water are scarce and male density is high, favorable egg-deposition sites should be rigorously defended. Despite much interest in the reproductive biology of *Phyllomedusa*, male-male behaviors have not been previously described in detail (but see Haddad and Giaretta 1999 for references to brief, unpublished accounts). Male-male interactions are important because the victors of these exchanges often achieve higher mating success than do their rivals (Duellman and Trueb 1986; Ryan 1985). Here we provide an account of site selection and defense, and male-male territorial behaviors in *P. sauvagii*.

MATERIALS AND METHODS

Phyllomedusa sauvagii were observed in a 3.5 m high grapefruit tree (*Citrus* sp.) with branches overhanging a backyard pool (2.0 x 3.0 x 0.8 m) in Yerba Buena, Tucumán Province, Argentina (26°48'41" S; 65°18'31" W; elevation 510 m).

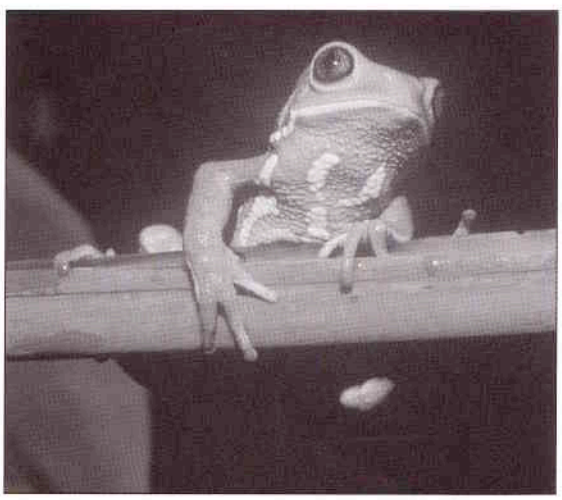

Figure 1. Male *Phyllomedusa sauvagii* in grapefruit tree, Yerba Buena, Tucumán Province, Argentina (courtesy of Richard Etheridge).

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Other anurans that regularly used and reproduced in the pool included *Bufo arenarum*, *Pleurodema borellii*, and *Scinax fuscovarius*. *Phyllomedusa sauvagii* had been observed returning to this tree each summer for several years. Systematic observations, including videotaping, were initiated during the summers of 1996–97 and 1997–98 (hereafter referred to as the first and second summer, respectively). Frogs were active from the end of October until mid-February during both summers. Observations lasted 95 nights during the first summer, and 78 nights the second summer. We observed the frogs with the aid of flashlights usually from 2100–2200 h which corresponded to periods of peak activity (unpubl. data). *Phyllomedusa sauvagii* did not appear to be at all disturbed by our lights or presence. Nevertheless, we avoided handling the animals (except on rare occasions when their identity could not be readily determined via visual inspection) fearing that they might not return on subsequent nights, or that such disturbances might interfere with their natural behaviors. Individual *P. sauvagii* were identified by their unique pattern of white streaks and spots on their throat and chest. Each night we identified the frogs that had returned to the area, and recorded their location and behavior. For location, we noted on which of the tree's three main branches (A, B, C) or offshoots the frogs were perched. The main branches forked from the trunk at approximately 1.5 m above ground. Only branch B and its offshoots were positioned over the pool. Therefore, optimum nesting sites appeared to be limited in this setting.

RESULTS

Activity and Branch Selection

Sixteen individuals were identified during the two summers of observations (nine males, three females, four of undetermined sex). Males positioned themselves on branches overhanging the pool (at about 1.5–2.0 m), or in a hedge that was in contact with the tree, and advertised their positions by vocalizing. Individuals frequently returned to the same position on the same branch on consecutive nights. Here, we limit our report of activity patterns and location selection primarily to four males (including the two most active individuals) for which we had gathered the most complete data.

Males #1 and #2 were observed on a similar number of nights during the first summer (37 and 40 nights, respectively; Table 1). Male #1 perched on branch B (over the pool) more often than did #2 (65% vs. 47.5%, respectively; Table 1). These two males were involved in 13 of the 18 recorded encounters (72%) for which the identity of males was known (of a total of 26 male-male encounters). Male # 1 was the 'winner' in seven of these 13 encounters (54%), four of which involved a 'losing' #2. We considered the winner to be the individual that returned to the contested position on the branch and the loser to be the male that departed the immediate area. In the other six encounters, #2 defeated #1 three times, #1 and #2 each lost to another male once (#4 and #6, respectively), and the outcome of the final encounter was undetermined. The other five encounters involved males not shown in Table 1. Male #2 was the only individual observed in amplexus the first summer.

The second summer, male #1 was seen only once (on branch C), whereas #2 appeared to be the new proprietor of branch B (Table 1). Most challenges to #2 were initiated by #3. We considered the initiator to be the frog that approached an individual that had previously established control of a calling site. Of 10 encounters for which the identity of the males was known (15 encounters in total), #2 was the winning male in three of these encounters. In fact, #2 was never observed to lose a fight that summer. Male #3 was seen in five encounters, twice with #2, twice with #6, and once with both 2 and 6. In each of these encounters #3 lost. During the second summer, seven pairs were observed in amplexus. One amplecting pair (female #22 and male #3), was joined by a third male (#2) that positioned himself on top of the pair. In this instance, it appeared as though both males may have been able to contribute sperm as the female oviposited.

On average, slightly fewer frogs were observed in the tree during the second summer than in the first. During the first summer, of the 63 nights in which at least one *P. sauvagii* was seen in the tree, we observed an average of 2.3 frogs per night (SD = 1.2; maximum 6). During the second summer, of the 46 nights in which at least one frog was present in the tree, we observed an average of 1.9 frogs per night (SD = 1.1; maximum 5).

Table 1. Number of times (with percentages in parentheses) four focal male *Phyllomedusa sauvagii* were seen on branches A, B (the over-water site), or C of the grapefruit tree during the two summers of observations. "Other" refers to locations either on the trunk or in a hedge that was in contact with the tree.

	Summer 1996–97					Summer 1997–98				
Frog	A	B	C	other	total	A	B	C	other	total
1	8 (22)	24 (65)	3 (8)	2 (5)	37 (100)	- (0)	- (0)	1 (100)	- (0)	1 (100)
2	3 (7.5)	19 (47.5)	10 (25)	8 (20)	40 (100)	1 (3)	23 (79)	3 (10)	2 (7)	29 (100)
3	- (0)	2 (18)	7 (64)	2 (18)	11 (100)	1 (7)	5 (33)	5 (33)	4 (27)	15 (100)
4	- (0)	2 (9)	11 (52)	8 (38)	21 (100)	- (0)	2 (25)	2 (25)	4 (50)	8 (100)

Agonistic Encounters and Visual Displays

Male *P. sauvagii* used visual displays and vocalizations during aggressive encounters. When an intruder male approached (within 0.2–0.5 m), the resident would walk toward him and, while facing the intruder, the resident very slowly stretched a hind leg in an arc, spreading the toes, and completely lengthening the leg posteriorly while raising it simultaneously 1–2 cm above the body (Fig. 2). The leg was then brought back alongside the body. This movement exposed the white markings along the ventral surface of the hind legs and lasted several seconds ($\bar{x} = 6.4 \pm 2.6$ sec; $n = 6$). We term this behavior a "leg-stretching" display. Intruders faced by a displaying male often did not retreat. The resident male would then slowly approach the intruder, all the while vocalizing, until physical contact was made. Of the 26 male-male encounters recorded during the first summer, we observed ten occasions in which leg-stretching displays preceded physical contact. Males that performed the leg-stretching displays were the winners in eight of ten physical encounters. Of the 15 encounters observed during the second summer, the two males that used leg-stretching displays prior to their physical encounters retained their positions. On two occasions we observed frogs performing leg-stretching displays which were not followed by physical encounters. In these situations, the intruder retreated prior to being approached by the resident male.

Physical encounters resembled a slow-motion wrestling match. Wrestling consisted of male-male grappling about the opponent's head and body using both the fore and hind limbs. One male would often climb atop his opponent so that his ventral surface would be against the back of his rival. On one occasion, two males were seen wrestling ventrum to ventrum, as one bit at the other's vocal sac. Fighting males remained in wrestling positions for 10–20 min. The apparent intent of the combatants was to dislodge their opponent from a favored position (usually a site on a branch overhanging water). Both males vocalized almost continuously during wrestling bouts with each using a different type of call.

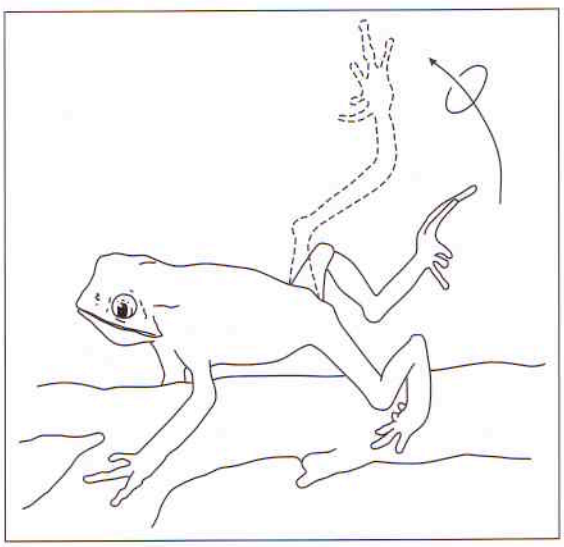

Figure 2. Two positions of the leg-stretch display in male *Phyllomedusa sauvagii*. Arrow indicates the direction of hind-leg extension and spreading and turning of the foot.

Wrestling bouts usually ended with the male on the bottom (the inferior position) releasing himself from the grip of the male above, and departing the immediate area. It is also possible that the male in the superior position loosened his grip to allow the male below to leave after hearing the release calls emitted by the bottom male. Of 12 physical encounters for which the outcome was known (of a total of 26 encounters observed during the first summer), in eight cases, the bottom frog managed to disengage and leave the area. In two instances, the male in the superior position left the area, and on two other occasions, the wrestling pair fell into the pool. During the second summer, six outcomes of 15 physical encounters were observed. On five occasions, the bottom frog left the area, and on one occasion, the top frog departed first.

Vocalizations

We distinguished three types of calls for *P. sauvagii*: advertisement, encounter, and release calls (Gerhardt 1994). On several occasions, resident males produced a call that sounded like a combination of the advertisement and encounter calls as they approached an intruder. Advertisement calls were made by males that occupied and defended the same branches on consecutive nights. Encounter calls were heard during male-male agonistic encounters, and were emitted by the male that was in the top position in a wrestling pair (i.e., usually the winning male). The male on the bottom invariably emitted a release call which, after a few minutes, seemed to result in the male above loosening his grip. This allowed the male below to disengage and retreat. Like other larger species of *Phyllomedusa*, the advertisement call of *P. sauvagii* is deep, loud, and unmodulated (Barrio 1976), and requires full inflation of the vocal sac. The frequency range for this call is broad (200–7000 Hz) with dominant frequencies ranging 500–3500 Hz (Barrio 1976). In contrast, encounter and release calls are lower-pitched calls which can be heard (at least by humans) only from short distances (maximum 2–3 m).

DISCUSSION

Male-male wrestling bouts, similar to what we observed in *P. sauvagii*, have been reported for other hylids including *Hyla melanargyrea* (Köhler and Böhme 1996) and four species of *Litoria* (Richards and James 1992). They have also been reported in the bufonid *Atelopus varius* (Crump 1988) and the leptodactylids *Eleutherodactylus urichi* (Wells 1981) and *Hylodes asper* (Haddad and Giaretta 1999). Agonistic encounters are usually preceded by vocalizations which are thought to function in localization of would-be competitors (e.g., Robertson 1986). Similar to our finding, Crump (1988) observed that in the bufonid *A. varius*, the calls used during encounters tended to be much less intense than were the advertisement calls. Goodman (1971) also reported that the calls emitted by fighting male *Dendrobates granuliferus* were of lower intensity.

In addition to vocalizations, some frogs use visual modes of communication in the form of bodily displays (Hödl and Amézquita, in press; Lindquist and Hetherington 1996). These visual signals may involve the front limbs, the hind limbs, or both (e.g., Haddad and Giaretta 1999; Harding 1982; Laurent 1973; Richards and James 1992). When vocalizations and visual displays are unsuccessful at thwarting a rival, encounters may escalate into physical contact (Fellers 1979; Mathis et al. 1995; Stebbins and Cohen 1995; Wells 1977) as was observed in *P. sauvagii*. The preference and aggressive defense for the branch position above the pool by the most competitively dominant males (Table 1) suggest that such sites are (1) in limited supply at this breeding site; and (2) may offer more breeding opportunities or greater reproductive success for males calling from these territories.

Territorial behaviors have been described in three other species of *Phyllomedusa*. In *P. hypochondrialis*, males perform a series of "hand-waving" behaviors prior to male-male encounters (Laurent 1973), and "leg signals" have been reported for *P. burmeisteri* (see Haddad and Giaretta 1999) and *P. distincta* (Castanho 1994, in Haddad and Giaretta 1999). Similar displays have been described for other frogs from several other families indicating that fore- and hind-limb displays have evolved independently in several frog lineages (Hödl and Amézquita, in press). A display similar to the leg-stretching behavior described here for *P. sauvagii* was described as a "foot-flagging" display by Richards and James (1992, and references there-

in) for Australian hylid frogs of the genus *Litoria*. In *Litoria*, the display involves either the front or hind limb, and may be associated with vibrations of the foot (Richards and James 1992). It is interesting that there exists similarities in the territorial behaviors of *Litoria* and *Phyllomedusa* given that other aspects of their biology are strongly convergent (e.g., ecophysiology; McClanahan and Shoemaker 1987; Withers et al. 1984).

Generally, agonistic visual displays are interpreted as a way of evaluating the size or general state of the opponent (Robertson 1986). In *P. sauvagii*, males that used the leg-stretching display retained their calling sites in 83% (10 of 12) of the ensuing physical encounters we observed. Hence, the leg-stretching display may be an important predictor of the outcome of physical encounters in this species. Yet despite this relationship, twelve intruders held their positions and ultimately engaged in agonistic physical encounters with the displaying resident. Perhaps these intruders did not consider the residents they challenged to be superior opponents. For that reason, rather than retreat, they chose to hold their position and ultimately wrestle for the favored calling site. The intruder's indifference to a displaying resident would be an evolutionarily stable strategy if the cost of the physical encounter was less than the potential for reproductive success once the favored calling site was secured (see also Ryan 1985). These conditions are likely met in this species and at this site because (1) physical encounters did not appear to cause physical injuries or to attract predators; and (2) there were a limited number of sites available for overwater nesting.

The fact that the leg-stretching display is performed at night and at distances of up to 0.5 m suggests that, to receive this signal, *P. sauvagii* must have reasonably well-developed night vision. This too is unusual because most frogs that perform visual displays are diurnal. Visually displaying frogs are thought to have evolved these 'alternative' behaviors because they live in environments with high ambient noise (e.g., along waterfalls or swift-flowing streams) which can interfere with auditory signals (Hödl and Amézquita, in press; Lindquist and Hetherington 1996). Thus it is curious to note that the leg-stretching display is present in *P. sauvagii*, a species known to reproduce only in association with still, quiet bodies of water (Lavilla and Scrocchi 1988). Perhaps this behavior evolved in response to the noisy environment produced by other species of calling frogs which breed in the same bodies of water. Alternatively, leg stretching could have evolved in an ancestor for other reasons (including those cited above) and has been retained within this species. Consequently, interpreting the role and evolutionary history of this visual display will require further studies.

Although several aspects of the reproductive biology of *P. sauvagii* and other phyllomedusine frogs are known, other questions remain unanswered. For example, do larger males tend to win in agonistic encounters? And, how do males determine that they are over water when they defend a territory and call to females? Likewise, how do pairs in amplexus determine if they are over water when they construct their leaf nests? Because these frogs can, at times, be seasonally and spatially abundant and appear to be undisturbed by the presence of observers, they provide exceptional candidates for behavioral studies and offer a wealth of opportunities for future research.

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NOTE ADDED IN PROOF

A recent paper (Ribeiro Matos et al. 2000, Herpetol. Rev. 31:84–86) describing similar vocalizations, calling-site fidelity, and agonistic encounters in *Phyllomedusa hypocondrialis* in northeastern Brazil appeared while our paper was in press.