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Breeding behaviour and mating success of *Phyllomedusa rohdei* (Anura, Hylidae) in south-eastern Brazil

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Abstract

Observations on the courtship behaviour, mating behaviour and mating success of a leaf-frog, *Phyllomedusa rohdei*, population were conducted in a temporary flooded site of the Atlantic Forest, south-eastern Brazil. We did not find any influence of size and body weight on male mating success across three scales: seasonal, nightly chorus and local groups (males found within 1 m of a mated pair). In addition, no evidence was found that female *Phyllomedusa rohdei* exhibit overt mate choice. The formation of mated pairs in *P. rohdei* occurred because males moved toward the females, rather than reverse. The only variable that was significantly related to male mating success was the number of nights of participation in chorus activity. Besides calling tactics, males showed active searching behaviour. There was no evidence of size- and mass-assortative mating, and a high percentage of fertilization at all size and mass ratios of males and females was observed. Clutches in this species are produced in the same manner found in others members of *Phyllomedusa*; a purse-like nest is made over water by folding a leaf around the egg mass (embryos and fluid-filled capsules). Finally, we supply a list of several studies that examined the relationship between size or mass ratios of males and females in amplexus and its influence on fertilization rate, and show that size-assortative mating in anurans is inconsistent (present in some species but not in other).

Keywords: *Anura, breeding biology, Hylidae, mating success,* Phyllomedusa rohdei

Introduction

Mate selection has been studied extensively in a great number of anuran amphibians (see Andersson 1994; Halliday and Tejedo 1995; Sullivan et al. 1995). Studies have examined the influence of body size (Davies and Halliday 1979; Howard and Kluge 1985; Morris 1989; Bastos and Haddad 1996), chorus tenure (Woodward 1982; Arak 1988; Sullivan and Hinshaw 1992; Murphy 1994) and calling behaviour (Sullivan 1983; Ryan 1985; Arak 1988; Cherry 1993) on male mating success. Traditionally, female choice and male–male competition have been identified as the mechanisms responsible for some patterns of non-random mating (Darwin 1859, 1871; Arak 1983; Halliday and Tejedo 1995; Sullivan et al. 1995), but recent studies have shown that they are not the only mechanisms of

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mate selection (see Andersson 1994; Murphy 1998). While contests between males is more important in explosive-breeding anurans, where large males achieve more matings as a result of their greater success in agonistic interactions (Davies and Halliday 1979; Howard and Kluge 1985), female choice occurs predominantly in prolonged-breeding anurans because of the greater opportunity for choice by females at the breeding sites (Ryan 1985; Sullivan and Hinshaw 1992; Bastos and Haddad 1996). However, the most important mechanism in prolonged breeders is endurance rivalry (see Sullivan et al. 1995).

Behavioural observations of both males and females prior to mating have been used to identify the ways in which pair formation occurs (initiation of amplexus behaviour), and consequently, how the mate selection operates (Arak 1988; Morris 1989; Bastos and Haddad 1996). The observation of initiation of amplexus can, for example, show whether females have the opportunity to choose their mates in species in which males engage in intense scrambles to obtain scarce females (Davies and Halliday 1979; Bastos and Haddad 1996). Behavioural observations are also important to verify how females sample males. During the reproductive period, females could assess all or only a few males at the pond (Ryan 1983; Arak 1988; Morris 1989; Wagner and Sullivan 1992; Murphy and Gerhardt 2002). As a result, comparisons of mated and unmated males over different temporal and spatial scales (e.g. over the course of a breeding season, within a night, within a local group) have been used to assess the presence of female choice, in order to test the influence of body size on mating advantage (see Ryan 1983; Morris 1989; Sullivan and Hinshaw 1992; Morrison et al. 2001).

We studied a prolonged breeding population of *Phyllomedusa rohdei* Mertens, 1926 for one breeding season and examined the influence of male body size, chorus tenure and male initial mass on mating success. We also examined the existence of size- and mass-assortative mating and examined whether fertilization success is affected by the relative size of members of a pair. We also present information on courtship and mating behaviour that has not been previously reported for this species.

Methods

Phyllomedusa rohdei was observed at a temporary pond of approximately 170 m^2, at Palmital (22°50′S, 42°27′W), Municipality of Saquarema, State of Rio de Janeiro, south-eastern Brazil, during 84 visits encompassing 411 h, from July 1999 to July 2000. On average, we remained at the pond for seven nights during each month. We visited the study area monthly when the pond was dry (from July 1999 to November 1999 and from March 2000 to July 2000) and fortnightly when the pond was flooded (from December 1999 to February 2000). Field observations were conducted from 17:00 h until approximately 24:00 h, depending on the activity of the frogs.

The snout–vent length (SVL) of individuals was measured to the nearest 0.1 mm with callipers and body weight was measured to the nearest 0.05 g with a Pesola® spring scale. Toe clipping marked individuals (Martof 1953); however, the opposable fingers (numbers 100 and 800) and toes (numbers 1 and 10) were not clipped. The height from the ground (vertical distribution) and distance from the water (horizontal distribution) were measured to the nearest 1.0 mm with a folding ruler 2.0 m long. Focal sampling and continuous recording were used for behavioural records of males and females in the breeding chorus (Martin and Bateson 1993). We used a stopwatch to measure the time of some behaviour displayed by individuals. Males captured in amplexus at the breeding pond were classified as cluster mated males (CMM, males with at least one single male within 1 m) or isolated mated males (IMM, males with all single males located more than 1 m distant).

To identify the scale at which possible female choice is acting, we compared the size of mated and unmated males at three scales: (1) seasonal (all mated males versus all unmated males captured in the breeding season); (2) nightly (all mated males versus all unmated males present in the chorus when we observed amplexus); and (3) local groups (CMM versus their unmated neighbours). Male body weight and nights spent in the chorus were analysed only in the first comparison. The first scale of analysis is commonly used in estimating phenotypic selection (Sullivan et al. 1995), whereas the latter two are scales at which females could potentially assess males' sizes (Ryan 1983; Murphy and Gerhardt 2002).

To measure fertilization success (herein, verified as the proportion of eggs that already developed into embryos or that initiated the development), pairs found in amplexus were placed into plastic bags containing a branch with appropriate leaves for oviposition and a little water from the pond. Clutches were maintained in the laboratory for 1 week, after which the number of embryos and non-developing eggs (an ovum) was counted.

Statistical procedures are taken from Zar (1999). Descriptive statistics are given as mean ± SD.

Results

Courtship and oviposition behaviour

Males of *Phyllomedusa rohdei* were found on the vegetation close to the ground (vertical distribution: 45.7 cm ± 32.6 from the ground, $n=155$) and near the pond's edge (horizontal distribution: 40.3 cm ± 23.3 from water, $n=112$). In courtship areas, calling or silent males moved around the adjacent vegetation or remained stationary on the same perch, moving the head or body constantly in different directions. Males ($n=11$) walked a mean distance of 101.7 cm ± 50.0, and males remained at the same perch for a mean time of 6.57 min ± 4.36 ($n=21$). Males called neither frequently nor simultaneously. Intervals between calling bouts lasted several minutes.

Mating behaviour can be described as follows. A female approaches the courtship area. She may continue moving around the vegetation ($n=12$) or directly search for a leaf above the water ($n=9$). When the female finds a leaf, she (alone) folds the leaf with her arms and legs (Figure 1; the leaf is not immediately glued) and may visit other leaves, until a male approaches and begins amplexus with her. Females folding leaves ($n=6$) were always intercepted by males, but they were occasionally (two out seven) intercepted by a male when moving in the vegetation. Males quickly approached females, sometimes emitting a subtle vocalization similar to advertisement calls. When more than one male approached a female, territorial calls, pursuing and physical combat sometimes ensued. Finally, when a male reached a female, he jumped on the female's back, initiating an axillary amplexus (Figure 2A). After starting amplexus, the pair can remain motionless or immediately begin oviposition. We observed the beginning of amplexus eight times, and in none of them did a female approach a male in an apparent solicitation of amplexus.

Once oviposition starts, the first eggs emerge on to the superior or inferior surfaces of the leaf near its inferior edge. As laying continues, the pair moves upward, pausing and intermittently releasing various eggs and eggless capsules (fluid-filled), and using their hind limbs to fold the leaf around the eggs, making a purse-like nest (Figure 2A). Immediately after the female liberates each egg, the male curves his body (Figure 2A) and aligns his cloaca with the female's. When the amplectant pair is close to the end of the leaf, the male leaves while the female remains (Figure 2B). The durations of three observed matings were 1 h 35 min, 1 h

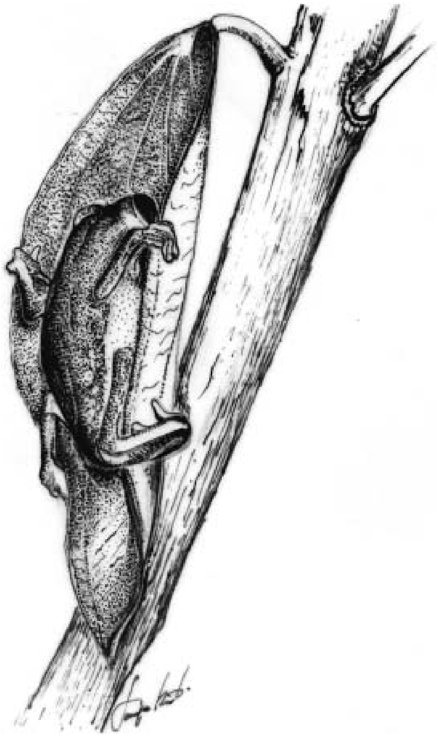

Figure 1. Female of *Phyllomedusa rohdei* folding a leaf with her arms and legs, before entering amplexus. At this moment, the leaf is not immediately glued (drawing from a photo).

45 min and 1 h 50 min. We observed pairs in amplexus between 19:00 and 03:00 h (n=20); the greatest number of the pairs (n=6) was found at approximately 23:00 h.

Clutches were found at a mean height of 79.5 cm ± 74.3 (n=21) above the water or ground. In general, there were eggless capsules in the upper and lower openings of the folded leaf. Eggs isolated from eggless capsules appeared to be dehydrated. Females deposited an average of 100 eggs ± 19 (n=30). The correlation between clutch size and SVL of females was not significant (Pearson correlation: r=0.30, P=0.10, n=30).

We observed three attempts by single males (unmated males) to displace males in amplexus. During these events, the single males pushed their snouts between the amplectant pair, using the vegetation around or the amplectant pair as support. In response, the mated male emitted short and quick vocalizations and threw kicks. Two solitary males did not succeed, but the third (SVL=39.9 mm) remained upon the mated male (SVL=37 mm) establishing a trio (Figure 2C). Oviposition followed normally.

Male mating success

We observed a total of 49 matings. Forty-one out 123 males (33.33%) mated once, and only eight males (6.5%) mated twice. The mean interval between matings for males that mated twice was 20.6 nights ± 11.7.

Figure 2. (A) A pair of *Phyllomedusa rohdei* in axillary amplexus folding a leaf (note the male curving his body to oppose the female's cloaca); (B) a female of *P. rohdei* alone at the end of oviposition; (C) trio during oviposition.


A
B
C

Non-random mating in *Phyllomedusa rohdei* was detected at the seasonal scale with respect to chorus tenure only (Table I). The multiple regression analysis of male size, body weight and chorus tenure on mating success of males showed that chorus tenure was the only variable significantly correlated with mating success (Table II).

Comparison of final body weight (weight that an individual male had in its last night in the chorus) with the initial body weight (weight that an individual male had in its first night in the chorus) shows that, on average, males of *P. rohdei* lost a mean of 10.2% ± 12.5 ($n=48$) of its weight during the breeding activities. The time interval over which these measurements was assessed (72.9 nights ± 48.9, $n=48$) is not correlated with the percentage of lost weight ($r=-0.09$, $P=0.56$).

For the 49 matings we observed, 55% ($n=27$) of mated males were classified as CMM, 37% ($n=18$) as IMM and for four males (8%) classification was not possible. The number of males present in each group ranged from two to six (3.2 ± 1.0). Clustered mated males (SVL, 39.2 mm ± 1.7, $n=23$) and IMM (SVL, 38.4 mm ± 2.9, $n=16$) did not differ significantly in size (Student's t test: $t=0.99$, $P=0.33$). The number of males present at the breeding pond was correlated positively with the number of CMM ($r=0.62$, $n=15$ nights, $P=0.01$), but not with the number of IMM ($r=0.14$, $P=0.61$), suggesting that aggregation of males in local groups may be a direct function of density and isolated males occur in any chorus size. Clustered mated males were not significantly larger than unmated neighbours (Table I). Likewise, on a nightly scale, mated males were not significantly larger than unmated males during 17 nights (Table I).

Table I. Comparisons of the size, body weight and chorus tenure of mated and unmated males of *Phyllomedusa rohdei* at the seasonal (Student's t test), nightly and local groups scales (paired t test).

(a) Seasonal scale	Mated males (MM)[a]	Unmated males (UM)[b]	
SVL (mm)	38.7 ± 2.2, $n=41$	38.1 ± 2.7, $n=82$	$t=1.23$, $P=0.22$
Body weight (g)	3.08 ± 0.46, $n=41$	2.97 ± 0.44, $n=71$	$t=1.27$, $P=0.21$
Number of nights	6.85 ± 4.54, $n=41$	5.01 ± 3.90, $n=82$	$t=2.34$, $P=0.02$
(b) Nightly scale	MM[a]	UM[c]	
SVL (mm)	39.2 ± 1.4	38.6 ± 0.4	
$n=14$ nights, diff. 0.5 ± 1.5, $t=1.39$, $P=0.19$			
(c) Local groups scale	CMM[d]	UMN[e]	
SVL (mm)	39.3 ± 1.1	39.1 ± 1.4	
$n=10$ groups, diff. 0.2 ± 1.8, $t=0.32$, $P=0.76$			

[a], [b] All mated and unmated males captured; [c] unmated males present on nights when amplexus took place; [d] clustered mated males; [e] unmated males neighbours.

Table II. Multiple regression of male mating success on snout–vent length (SVL), body weight and the number of nights spent at the pond.

Independent variables	β	SE	t value	P
SVL (mm)	0.12	0.14	0.87	0.38
Body weight (g)	−0.03	0.14	−0.17	0.86
Number of nights	0.30	0.10	3.00	0.003

β, standardized regression coefficient; SE, standard error of β. Dependent variable: male mating success [$R^2=0.096$, $F=3.83$, $P<0.01$, $N=112$ (Durbin–Watson $d=1.818$, serial correlation of residuals=0.068)].

There was no evidence of size and mass-assortative mating; correlations between size ($r=-0.08$, $P=0.50$, $n=48$) and mass ($r=0.05$, $P=0.70$, $n=31$) of males and females in amplexus were not significant. The percentage of eggs fertilized in clutches was high (99.7% ± 1.1, $n=19$).

Discussion

The hypothesis that females mate with larger or heavier males was not supported in our study. Moreover, mated males were not larger than unmated males at the scales females could have assessed males: local groups and the nightly chorus. Random mating with respect to size appears to be very common in anuran amphibians (see review by Halliday and Tejedo 1995), occurring in both prolonged and explosive breeders of diverse genera. The only variable that was significantly related to male mating success was chorus tenure. A great number of studies have documented significant correlations between male mating success and the number of nights of participation in chorus activity (e.g. Woodward 1982; Ryan 1983; Arak 1988; Morris 1989; Sullivan and Hinshaw 1992; Cherry 1993; Martins 1993; Murphy 1994). Variation among males in chorus tenure may be explained by variance in the ability of males to meet the physiological demands of mating activity. Our results agree with Halliday and Tejedo's (1995) ideas, indicating that sexual and competitive behaviour is energetically expensive for male anurans as evidenced by substantial weight loss during the mating period. Furthermore, in some species (e.g. *Hyla gratiosa*; Murphy 1994) male stamina can affect mating success by the simple addition of nightly probabilities of mating with a female (Halliday and Tejedo 1995).

Males of *P. rohdei* in the studied population adopted two mating tactics: calling and patrolling behaviour (apparently similar to active searching behaviour, *sensu* Wells 1977). The latter seems to occur in other species of the subfamily Phyllomedusinae: *Agalychnis callidryas* and *Pachymedusa dacnicolor* (Pyburn 1970), *Phyllomedusa boliviana* (Vaira 2001), *P. burmeisteri* (Abrunhosa and Wogel 2004), *P. distincta* (Castanho 1994), *P. hypochondrialis* (Pyburn and Glidewell 1971; Matos et al. 2000), and *P. lemur* (Jungfer and Weygoldt 1994). The evolution of patrolling behaviour, at least in *P. rodhei*, could be related to the low calling rates of males. Low calling rates could make it difficult for females to locate males, making the search for mates costly. As a result, females would not move in courtship areas in order to find a male, but to find an adequate leaf on which to oviposit. Indeed, our observations support this conclusion. The formation of pairs in amplexus, in *P. rohdei*, occurred because males moved toward the females, not the reverse. In this case, scramble competition (or interaction-independent sexual selection *sensu* Murphy 1998) could be responsible for pair formation, so that a higher mating success would be associated with males' ability in maintaining neighbours apart and/or finding females quickly. A simpler alternative hypothesis suggests that the searching by females for oviposition sites selects for male patrolling behaviour, and that low call rates are sufficient to keep rival males at a distance.

The clutches of *P. rohdei* follow the same pattern found in other species of the genus *Phyllomedusa* (e.g. Pyburn and Glidewell 1971; Pyburn 1980; Langone et al. 1985; Matos et al. 2000; Vaira 2001; for exception see Jungfer and Weygoldt 1994): a purse-like nest is made over water by folding a leaf around the egg mass-embryos and fluid-filled capsules. The eggs located next to the openings of the folded leaf without eggless capsules around them were dehydrated. This observation support Pyburn's (1980) conclusions that these eggless capsules prevent drying and death of embryos during the prehatch period.

Various studies have demonstrated a positive correlation between female clutch size and SVL (see Salthe and Duellman 1973; Martins 1988; Bastos and Haddad 1996), but this was not the case for *P. rohdei*. Since some females were able to attend more than once in the breeding pond (Wogel et al. forthcoming), our results may be related to a decrease in the number of eggs at each oviposition.

Because of the occurrence of external fertilization in anuran amphibians, an association between body sizes of mates has been proposed (Licht 1976), as similar body sizes should facilitate fertilization (Davies and Halliday 1977). Nevertheless, size-assortative mating in anurans is inconsistent (present in some species but not in others; Table III), and the mechanisms responsible for this variation are still not known. Some authors (Davies and

Table III. List of some studies that examined the relationship between size (S) or mass (M) ratios of males and females in amplexus and/or its influence on fertilization rate.

Species	Assortative mating	Fertilization success	References
Alytes obstetricans	P (S)	–	Böll and Linsenmair (1998)
Bufo americanus	–	IR	Kruse and Mounce (1982)[a]
Bufo boreas	P (S)	–	Olson et al. (1986)[b]
Bufo bufo	A (S)	–	Marco and Lizana (2002)
Bufo bufo	A (S)	IR	Höglund and Robertson (1987)
Bufo calamita	A (S)	–	Arak (1988)
Bufo calamita	–	IR	Tejedo (1992)
Bufo cognatus	–	IR	Krupa (1988)
Bufo fowleri	A (S)	–	Fairchild (1981)
Bufo terrestris	A (S)	–	Wilbur et al. (1978)
Bufo terrestris × *B. americanus*	A (S)	–	Wilbur et al. (1978)
Bufo typhonius	A (S)	–	Wells (1979)
Bufo valliceps	A (S)	–	Wagner and Sullivan (1995)
Bufo woodhousei	P (S), A (S)	–	Sullivan (1987)[c]
Hyla chrysoscelis	A (S)	–	Morris (1989)
Hyla chrysoscelis	A (S)	–	Godwin and Roble (1983)
Hyla cinerea	A (S)	IR	Gerhardt et al. (1987)
Hyla elegans	P (S)	OR, $r=0.81$	Bastos and Haddad (1996)
Hyla labialis	P (S)	–	Lüddecke (2001)[d]
Hyperolius marmoratus	A (S)	IR	Telford and Dyson (1988)[e]
Hyperolius marmoratus	A (S)	–	Dyson et al. (1992)
Pelobates cultripes	A (S)	–	Lizana et al. (1994)
Phyllomedusa boliviana	A (S)	–	Vaira (2001)
Phyllomedusa rohdei	A (S, M)	IR	This study
Physalaemus cuqui	A (S)	–	Ferrari and Vaira (2001)
Physalaemus enesefae	P (S)	–	Tárano and Herrera (2003)
Physalaemus pustulosus	A (S)	OR	Ryan (1983)[f]
Rana temporaria	–	OR	Gibbons and McCarthy (1986)[g]
Rana temporaria	A (S)	IR	Elmberg (1991)
Scinax rizibilis	P (S, M)	–	Bastos and Haddad (1999)
Scinax rubra	P (S)	OR, $r=0.80$	Bourne (1993)
Uperoleia rugosa	P (M)	OR, $r=0.64$–0.80	Robertson (1986, 1990)

Assortative mating: P, present or A, absent. If present, r means the optimal male–female size ratio that maximizes fertilization rate. Fertilization success: OR, attained in optimal ratio or IR, attained independent of the pairs' size ratios. [a]Although data are incomplete, a high fertilization efficiency was attained by males of different sizes; [b]see other references in this study; [c]occurrence of inter-season variation; [d]only when male availability per female was moderately high; [e]information if fertilization ratio was high or low was not provided; [f] just for large females; [g]an optimal ratio value was not provided by authors.

Halliday 1977; Robertson 1990; Bourne 1993; Bastos and Haddad 1996) have suggested that in species with axillary amplexus, males with 60–80% of the female body size should be more successful than others in fertilizing all or almost all eggs. We hypothesize that in some species pairs may be able to closely align cloacae by performing special postures during egg laying. *Bufo cognatus* (Krupa 1988, and references therein) provides a fine example. In this species, fertilization efficiency was high and independent of the pairs' size ratios. Krupa (1988) suggested that this success may be the result of the basket posture exhibited by pairs in amplexus. During oviposition, males of *P. rohdei* curve their bodies as eggs are extruded, matching their cloacae to those of their mates, and a high fertilization rate is attained at any size ratio. Preventing males from curving their bodies during oviposition could test this hypothesis.

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