

CHORUS ORGANIZATION OF THE LEAF-FROG *PHYLLOMEDUSA ROHDEI* (ANURA, HYLIDAE)

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We studied the chorus organization of a population of prolonged-breeding *Phyllomedusa rohdei* at a temporary pond in Saquarema, State of Rio de Janeiro, south-eastern Brazil. Males, females and amplexant pairs were more abundant when the pond filled up for the first time (in December 1999). We found a positive correlation between the number of males and females in the chorus, but no significant correlation between operational sex ratio and the number of males present. The number of nights that males participated in a breeding chorus was shortened. The ability to remain in breeding aggregations was not correlated with the snout-vent length of males, but it was correlated with the initial body weight. Males showed high site fidelity and some turnover between consecutive nights. Larger males predominated in the chorus when there was water in the pond, while smaller males predominated when the pond was dry. The spatial distribution of males in the pond was clustered; aggregations occurred in places with adequate oviposition sites for this species. *Phyllomedusa rohdei* was not considered a lek species mainly because male territories enclose oviposition sites.

Key words: mating system, reproductive biology, spatial distribution, temporal distribution

INTRODUCTION

Numerous aspects of the social behaviour of anuran amphibians are related to breeding activities (Wells, 1977a; Heatwole & Sullivan, 1995). In general, reproductive activities of anuran species are announced by a congregation of calling males in dense choruses in a flooded area (Wells, 1977a). The primary role of these communal displays appears to be enhancement of attractiveness through the increase in volume and in the active space of the signal (Wilson, 1975). However, at a fine scale within breeding sites, the aggregative behaviour of males can be explained by several factors (see Pfennig *et al.*, 2000, and references therein). In anurans, the mechanisms responsible for aggregative behaviour of males seem to be mainly associated with sexual parasitism (Perril *et al.*, 1978; Haddad, 1991; Pfennig, *et al.*, 2000), and/or to promote the reduction of individual's risk of predation (Ryan *et al.*, 1981; Pfennig *et al.*, 2000).

A lek is usually defined as a communal sexual display area where males congregate for the purpose of attracting and courting females and to which females come for mating (Wilson, 1975). In these areas, males do not control resources critical to females, and except for their contribution of sperm, males provide no parental care for the eggs or young (Bradbury, 1981). Bradbury (1981) listed conditions to characterize a lek species. Based on it, many anurans aggregations can be classified as leks mainly because oviposition occurs away from the immediate vicinity of the calling site of males, and males provided only sperm to female mates (e.g.

Ryan, 1985; Arak, 1988; Bourne, 1992; Bastos & Haddad, 1996).

Emlen & Oring (1977) and Wells (1977a) pointed out that the length of the breeding period influences the reproductive behaviour of the species. In general, temperature and rainfall have been considered as the most important environmental factors responsible for the length of the breeding period in anuran species (e.g. Salvador & Carrascal, 1990; Lizana *et al.*, 1994; Pombal, 1997). Nevertheless, the specific environmental conditions that dictate chorus attendance by males and females in breeding sites have rarely been investigated (see Sinsch, 1988; Ritke *et al.*, 1992; Henzi *et al.*, 1995; Murphy, 2003 for exceptions).

Either in prolonged or explosive breeders (*sensu* Wells, 1977a), the number of nights that a male is present in breeding aggregation (male chorus tenure) is quite abbreviated with respect to the length of the breeding season (Ryan, 1985; Murphy, 1994a). Explanation of this pattern has centered on energy limitations to sustain the high energetic cost of calling activities (Bucher *et al.*, 1982; Murphy, 1994b; Given, 2002). More specifically, some studies showed that the energy reserves obtained before the breeding period were responsible for male chorus tenure (e.g. Green, 1990; Murphy, 1994b). Nevertheless, in spite of this high tendency to non-attendance, every night new males come to breeding sites renewing the chorus from night to night. In this sense, males may present a high (Dyson *et al.*, 1992 – *Hyperolius marmoratus*) or a low turnover (Gerhardt *et al.*, 1987 – *Hyla cinerea*).

In this paper, we examine several aspects of chorus organization of *Phyllomedusa rohdei* Mertens focusing mainly on (1) the temporal and spatial distributions in both sexes, (2) the pattern of dispersion (uniform, random, or clumped) of males, and its possible causes, (3)

the influence of environmental variables (pond depth, air temperature and rainfall) on attendance of males, females and amplexant pairs in the pond, (3) the number of nights that males and females spent in breeding aggregations, and (4) the occurrence of site fidelity displayed by males, as well as lek behaviour based on Bradbury's conditions.

MATERIALS AND METHODS

STUDY SITE AND GENERAL FIELDWORK

A population of *Phyllomedusa rohdei* was studied at Palmital (22°50'S; 42°27'W), Municipality of Saquarema, State of Rio de Janeiro, south-eastern Brazil, from July 1999 to July 2000. The study site was a temporary pond of approximately 170 m². The pond has an approximately rectangular shape, having in its central area a small portion of land covered by vegetation which was connected to the mainland by a narrow pathway. The fieldwork was carried out 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). Each trip consisted of one to seven consecutive nights of study. We monitored the pond for a total of 411 hours in 84 visits. Field observations were conducted from 1700 hr until 2400 hr, depending on the activity of leaf-frogs.

To evaluate the level of site fidelity of males, each segment of the pond was divided into three parts of approximately 3 m wide. Individuals captured within the same area on at least two consecutive nights were considered to exhibit site fidelity. For all collected individuals we measured the snout-vent length (SVL) to the nearest 0.1 mm with caliper ruler and weighed individuals to the nearest 0.05 g with a Pesola® spring scale. We marked the leaf-frogs individually by toe clipping (Martof, 1953). The opposable fingers (numbers 100 and 800) and toes (numbers 1 and 10) were not clipped.

SURVEY OF SPATIAL DISTRIBUTION

By categorizing two physical characteristics of the pond margin (vegetation cover classified as dense or scarce; and availability of oviposition sites as with or without oviposition sites), we recognized four microhabitats: dense vegetation with oviposition sites (DWS); dense vegetation without oviposition sites (DWS); scarce vegetation with oviposition sites (SWS) and scarce vegetation without oviposition sites (SWS). Adequate oviposition sites for *P. rohdei* were defined as leaves of a width equal to or larger than the width of a female and that could be folded by them (i.e. leaf width did not exceed the width of a female with its arms stretched). The microhabitat DWS was the largest, representing 41.8% from the pond edge (DWS 18.5%; SWS 11.9%; SWS 27.9%). The vegetation in the middle of pond and beyond the microhabitats area was not considered. The individuals were only observed on the edge of the pond. In December 1999 the mean

pond depth was 70.4±9.8 cm ($n=11$); in January 2000, 27.8±9.5 cm ($n=6$) and in February 2000, 14.1±1.5 cm ($n=5$). The air temperature was recorded in the study area at 1.5 m high. Pluviometric data (amount of rain for the month) were recorded at the Estação Rio Mole (22°51'S; 42°33'W), located approximately 10 km from study area. We performed a multiple regression analysis to assess the influence of pond depth, air temperature, and rainfall on number of males, females, and amplexant pairs using a forward stepwise method, allowing an evaluation of the relative contribution to attendance of both sexes and amplexant pairs of the three specific environmental variables (pond depth, air temperature and rainfall).

Over five nights at 2100 hr (time of the highest calling activity of males), we intensively searched for males at the calling sites. The individual positions of calling males were plotted in a schematic map, where the spatial distribution of males was determined using a Poisson distribution test. We used two methods (see Brower & Zar, 1984) to verify whether males were randomly distributed: (1) the "variance-to-mean ratio", where we calculated a χ^2 value as the sum of squares of the samples divided by the sample mean. A ratio (or coefficient of dispersion) less than 1.0 indicates a uniform distribution, and a ratio greater than 1.0 indicates clumping; and (2) the "goodness-of-fit test": to test if the observed frequencies deviate significantly from the frequencies expected by the null hypothesis of randomness, we employed a χ^2 test computed as $\Sigma(f - F)^2 / F$, where f is an observed frequency and F is its associated expected, or hypothesized, frequency.

Field methods and statistical procedures are taken primarily from Brower & Zar (1984) and Zar (1999). Non-parametric statistical tests were employed when assumptions of normality were violated. Descriptive statistics are given as mean ±SD for parametrical data and medians, range for non-parametrical data.

RESULTS

POPULATION STRUCTURE

We marked a total of 143 males and 69 females during the study. Females (SVL 44.4 mm, range 37.5-50.2 mm, $n=69$; mass 4.10 g, range 2.45-6.60 g, $n=57$) were longer (Mann-Whitney $U = 330.0$, $P < 0.01$) and heavier ($U = 579.0$, $P < 0.01$) than males (SVL 38.4 mm, range 25.0-45.0 mm, $n=143$; mass 2.95 g, range 1.50-4.40 g, $n=121$).

Males were observed calling across the year (from July 1999 to May 2000). However, only in December 1999 did the number of males and females increase quickly and only between December 1999 to March 2000 did we observe amplexant pairs (Fig. 1). Chorus duration and number of males calling during the night were greater in the months when the pond was flooded (December 1999, January and February 2000). The nocturnal activity peak of males (time of the greatest number of males calling) was at 2000 hr when the pond

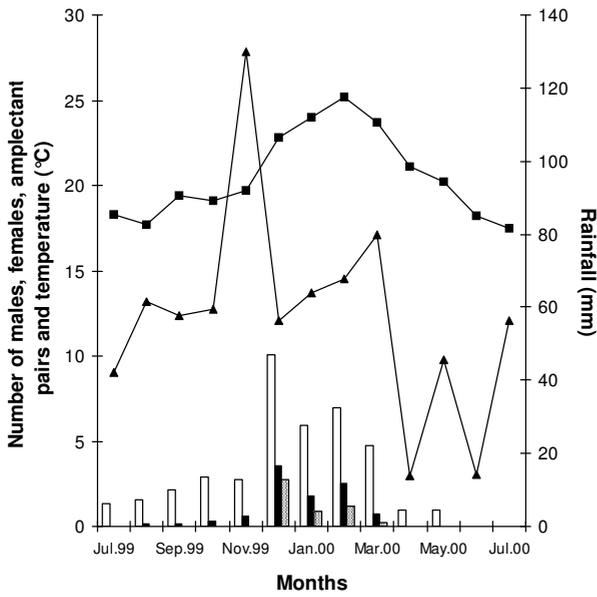


FIG. 1. Number of males (white columns), females (black columns), and amplexant pairs (dotted columns) of the *Phyllomedusa rohdei*, and air temperature (squares) and rainfall (triangles) at a temporary pond in Saquarema, State of Rio de Janeiro, south-eastern Brazil from July 1999 to July 2000.

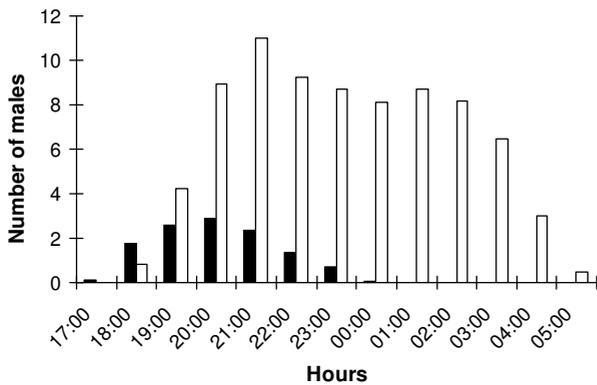


FIG. 2. Mean number of calling males of *Phyllomedusa rohdei* along the night in the months of dry pond (black columns) and in the months of flooded pond (white columns) at a temporary pond in Saquarema, State of Rio de Janeiro, south-eastern Brazil.

was dry and at 2100 hr when the pond was flooded (Fig. 2). Males of *P. rohdei* were found over the vegetation close to water (vertical distribution: mean = 45.7 ± 32.6

TABLE 1. Correlations (Pearson correlation coefficient) between pond depth (PD), air temperature (AT), rainfall (RF), and number of males (NM), number of females (NF), and amplexant pairs (AP), at a temporary pond in Saquarema, State of Rio de Janeiro, south-eastern Brazil, and results of forward multiple regression analyses [Beta coefficient (Beta) and partial correlation (pc)]. * $P < 0.05$

	Correlations (r)			NM		NF		AP	
	NM	NF	AP	Beta	pc	Beta	pc	Beta	pc
PD	0.87*	0.80*	0.97*	0.69*	0.89*	0.51*	0.82*	0.90*	0.96*
AT	0.73*	0.82*	0.59*	0.35*	0.69*	0.54*	0.84*	0.13	0.48
RF	0.27	0.31	0.05	0.18	0.48	0.19	0.52	—	—
Regression results				$R^2=0.90^*$		$R^2=0.91^*$		$R^2=0.96$	
				$F_{3,9}=28.16$		$F_{3,9}=30.0^*$		$F_{2,10}=107.80$	

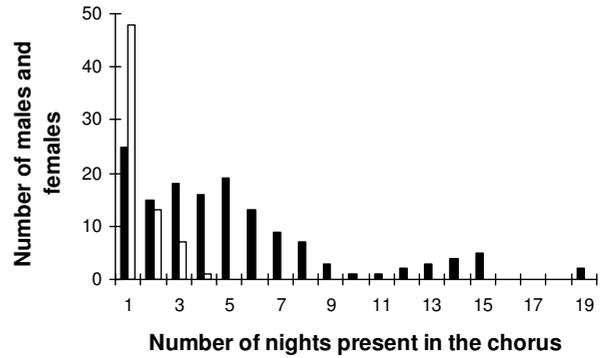


FIG. 3. Number of nights that individual males (black columns) and females (white columns) of *Phyllomedusa rohdei* attended a pond chorus between July 1999 and March 2000 in a temporary pond in Saquarema, State of Rio de Janeiro, south-eastern Brazil.

cm from the ground, $n=155$) and on the pond's edge (horizontal distribution: mean = 40.3 ± 23.3 cm from water, $n=112$).

The number of males found in 19 nights ranged from 8 to 61 (mean = 26.6 ± 14.3) and the number of females ranged from 0 to 10 (mean = 4.6 ± 2.9). The operational sex ratio (OSR: number of reproducing females/ number of reproducing males) in the population of *P. rohdei* was highly male-biased (mean = 0.19 ± 0.10 , $n=19$ nights). The number of females was positively correlated with the number of males in the chorus (Pearson correlation; $r=0.7$, $P < 0.05$, $n=19$ nights), however the OSRs were not significantly correlated with the number of males present in the chorus ($r=-0.32$, $P > 0.05$, $n=19$ nights), indicating that females were not proportionally more abundant in larger choruses. Correlation matrices and the multiple regression analysis are presented in Table 1. In general, the results of correlations (Pearson correlation coefficient) between pond depth (PD), air temperature (AT), rainfall (RF) and number of males (NM), females (NF) and amplexant pairs (AP) and multiple regression analyses were similar. The PD and AT were significantly correlated with NM, NF, and AP. Surprisingly, the RF was not significantly correlated with either of dependent variables. An evaluation of Beta coefficients and partial correlations between these variables reinforced the relative contribution of PD and AT in predict the NM and NF, and only PD for AP, when controlling the effect of other variables.

TABLE 2. Percentage of males (M), females (F), and amplexant pairs (AP) of *Phyllomedusa rohdei* present in each microhabitat (Mi) in a temporary pond in Saquarema, State of Rio de Janeiro, southeastern Brazil. M/Mi: % of males/% of length of microhabitat; F/Mi: % of females/% of length of microhabitat; P/Mi: % of amplexus pair / % of length of microhabitat. DWS: dense vegetation with oviposition sites; DWoS: dense vegetation without oviposition sites; SWS: scarce vegetation with oviposition sites; SWoS: scarce vegetation without oviposition sites.

Microhabitat	Males	M/Mi	Females	F/Mi	Amplexant pairs	AP/Mi
DWS	68.71%	1.65	70.21%	1.69	78.73%	1.89
DWoS	5.59%	0.30	9.57%	0.52	4.25%	0.23
SWS	15.27%	1.28	14.89%	1.25	14.89%	1.25
SWoS	10.43%	0.37	5.32%	0.19	2.13%	0.08
Total number	537 males	—	94 females	—	47 pairs	—
Nights sampled	14		17		17	

The male chorus tenure (Fig. 3) was abbreviated (4.0, range 1.0-19.0, $n=143$), representing 6.2% of the length of the study season (84 nights sampled). There was no correlation between SVL of males and the number of nights in the chorus (Spearman Rank-correlation; $r_s=0.15$, $P>0.05$, $n=143$), but we found a positive correlation between initial mass of males (mass observed on the first night in the chorus) and the number of nights in the chorus ($r_s=0.31$, $P<0.01$, $n=120$).

Females attended (1.0, range 1.0-4.0, $n=69$) fewer nights than males in the chorus ($U=1436.0$, $P<0.01$). About 70% of females spent a single night in the pond (Fig. 3). Females were present in the chorus on 26 nights (37.7% of the duration of this study, $n=69$ nights sampled). Amplexant pairs were found in 18 nights (26.1% of total). The mean number of days between two recaptures of females from December 1999 to March 2000 was 29.1 nights \pm 28.4 ($n=20$). Of 12 females which returned to the breeding site with intervals above 20 nights, about 70% were first captured in December 1999 (25% in January 2000, and 5% in February 2000). Only three females mated twice; the intervals between the ovipositions were 26, 32, and 60 days (these females first mated in December 1999). The number of eggs deposited by one of these females in the first capture was 140 eggs and in the recapture were 104.

About 45% of males (range 20-70%; $n=12$ pairs of two consecutive nights) present in one night were present in the next night. On average, the chorus on any night was formed by 40% (range 10-80%) of males present in the previous night and 60% (range 20-90%) of males that did not participated in the chorus of the

previous night. The degree of site fidelity displayed by males was high. Nearly 70% of males were found in the same place they occupied in the previous night. Individual males remained for eight nights within the same area. Males that displayed site fidelity were not significantly larger (mean = 39.0 \pm 2.4 mm, $n=76$) than males that moved out to other sites on the following night (mean = 38.5 \pm 2.5 mm, $n=39$, $t=0.95$, $P=0.34$).

The mean body size of males that were present during the dry pond periods (July 1999 to November 1999 and March 2000) (38.0 mm, range 25.0-45.0, $n=70$) was significantly smaller ($U=5604$; $P=0.0004$) than that of males that were present at the pond when it had water (December 1999, January and February 2000) (38.6 mm, range 27.1-45.0, $n=223$). The mean SVL of males among the months with water in the pond did not differ significantly (Kruskal-Wallis test: $H_{(2,n=223)}=0.38$, $P=0.83$; Median test: $\chi^2=0.25$, $df=2$, $P=0.88$).

SPATIAL DISTRIBUTION

The number of males, females, and amplexant pairs observed varied among each microhabitat (Table 2). There were more males, females, and amplexant pairs in the DWS than in other microhabitats. In these places, males performed their breeding activities, ousting intruders, attracting females, and mating. In general, the spatial distribution of males in the pond was clustered (Table 3). Both methods showed a tendency towards a clumped distribution pattern, except for two nights (21 and 29 December 1999). The mean SVL of males of the microhabitats with oviposition sites (39.0 mm, range 27.1-45.0, $n=437$) did not differ ($U=21207.5$, $P=0.88$)

TABLE 3. Coefficient of dispersion (CD, variance-to-mean ratio) and goodness-of-fit test for males of *Phyllomedusa rohdei* attending choruses at a temporary pond in Saquarema, State of Rio de Janeiro, south-eastern Brazil over 5 nights of breeding activity with different chorus size, as indicated by the Poisson distribution. * $\chi^2_{0.05,186}=216.55$ (critical values of the chi-square distribution), † $P < 0.05$.

Date	Variance-to-mean ratio			Goodness-of-fit
	Chorus size	CD	χ^2_1 *	$\chi^2_{2, P}$ -level (df)
11/12/1999	21	1.40	260.39†	1000.35, $P=0.001$ (3)
13/12/1999	27	1.35	250.75†	333.10, $P=0.001$ (3)
21/12/1999	30	1.25	232.42†	4.78, $P=0.19$ (3)
29/12/1999	32	1.18	218.61†	1.48, $P=0.48$ (2)
2/01/2000	45	1.30	242.38†	105.79, $P=0.001$ (3)

from the mean SVL of males of the microhabitats without oviposition sites (39.0 mm, range 26.0–42.6, $n=98$).

DISCUSSION

Despite the apparent disorder in breeding sites of *Phyllomedusa rohdei*, chorus exhibits some organization. The studied population exhibited typical patterns of prolonged breeders (*sensu* Wells, 1977a), having a long breeding season with relatively low male densities, asynchronous arrival of females at the breeding pond, and a strongly male-biased operational sex ratio. Although calling activities were not restricted to the rainy season, males were more abundant and allocated more time during it. We did not detect changes in the size distributions of individuals within a breeding season as observed for other species by several authors (e.g. Howard, 1978 – *Rana catesbeiana*; Sullivan, 1987 – *Bufo woodhousei*; Salvador & Carrascal, 1990 – *Bufo calamita*, *Hyla arborea*, *Pelobates cultripes*, *Rana perezi*; Lizana *et al.*, 1994 – *Pelobates cultripes*). However, compared to the dry period, larger males were more frequent in the three months when there was water in the pond. Chorus attendance by small males before or during late breeding season could reduce competition and possible injuries with larger males (Salvador & Carrascal, 1990; Lizana *et al.*, 1994). Considering the short period in which the breeding sites are available and consequently the restricted opportunity for reproduction, presumably only larger males would be successful in reproductive aggregations, if territorial defence is important.

Phyllomedusa rohdei males showed significant clumping within breeding ponds. Our results suggest that aggregations by *P. rohdei* males occur, at least in part, because they preferentially cluster in areas through which the largest number of females is likely to pass. This behaviour resembles the hotspot model which predicts that aggregations are formed by the product of attempts of males to display courtship behaviour in certain locations such as foraging, nesting or roosting sites where females may be found more easily and more abundantly (Bradbury & Gibson, 1983; Beehler & Foster, 1988). These areas preferred by both sexes had adequate oviposition sites. Yet, if microhabitats with oviposition sites afford more mating success than others (in this study: without oviposition sites), so the selection would favour larger and stronger males in the microhabitats with oviposition sites. Despite what has been demonstrated in some studies (e.g. Wells, 1977b; Howard, 1978), our results do not corroborate this hypothesis. The difference in male size between microhabitats with and without adequate oviposition sites was not significant, suggesting that larger males do not predominate in better areas.

Approximately half of the males present on any one night did not participate in the chorus of the previous night, a medium turnover rate when compared with other species (Gerhardt *et al.*, 1987; Dyson *et al.*, 1992).

The chorus tenure of *P. rohdei* males at the breeding site was shortened with respect to the length of the breeding season. This low attendance in choruses has been also observed in several species (e.g. Ryan, 1985; Murphy, 1994a). Since there was a positive correlation between initial mass of males and number of nights present in the chorus, we suggest that energy reserves accumulated before or during the beginning of the chorus can limit male attendance. A similar conclusion was found by Green (1990) and Murphy (1994b). Although chorus tenure of males had been abbreviated, they had greater attendance than females, on average, almost four times as many nights. Woodward (1984) suggested two reasons to explain why males spend more nights in the pond than females: (1) it is harder for a male than a female to obtain a mate and (2) males can mate more times than females in breeding season.

The absolute number of females arriving at the breeding site was correlated with chorus size, but larger choruses did not attract proportionally more females per male. Several studies have found similar results (e.g. Arak, 1988; Dyson *et al.*, 1992; Bastos & Haddad, 1996). Three possible explanations for the positive correlation between the number of males and females in the chorus are: (1) large choruses are more audible, therefore attracting more females (Wells, 1977a), (2) female preference for larger aggregations: females prefer to select males from larger choruses because they provide a greater range of choice (Bradbury, 1981; Ryan *et al.*, 1981) or (3) the movement to a pond is triggered by the same climatic factors in both sexes (Arak, 1988; Sinsch, 1988; Murphy, 2003). Vocalizations of *P. rohdei* males in breeding aggregations are somewhat infrequent, with long silent intervals between calls, which there is no a loud chorus. Perhaps this calling behaviour decreases the ability of females to estimate the chorus size through chorus intensity (Wells, 1977a; Bradbury *et al.*, 1981; Henzi *et al.*, 1995), suggesting that the first hypothesis above can be discarded or simply females appear not to assess the number of calling males by the intensity of signal output of a chorus (Murphy, 2003). Although the number of environmental variables recorded was somewhat restricted compared to other studies (e.g. Sinsch, 1988; Henzi *et al.*, 1995; Murphy, 2003), our data indicate that the movement of males and females to the pond can, in part, be explained by the influence of environmental variables – specifically, pond depth and air temperature. Pond depth can be considered an indirect measure of previous rainfall. In fact, more precipitation was registered in November 1999 (last days). Hence, the apparent lack of the influence of rainfall on reproductive activities of *P. rohdei* is misleading, because it was only after rain (December 1999) individuals moved to pond. In light of the data, the second explanation should not be discarded.

Twenty out of 69 females (29%) were observed twice at the breeding site. From this total, only three females mated twice. About 70% of females observed twice at

the breeding site were first captured in December 1999. The potential to breed twice in *P. rohdei* (and in other anurans with prolonged breeding) may be determined by the early arrival in the breeding season, in order to have sufficient time to produce another clutch. According to Telford & Dyson (1990), a possible constraint on anurans producing more than one egg clutch during a single breeding season is the time required to acquire sufficient energy to produce a new clutch. Thus, the ability of females to arrive early in the breeding season may be an adaptive character, especially in temporary habitats, where this behaviour may be associated with increased reproductive success.

The presence of an individual at the same position in the pond (site fidelity) has been considered as territorial behaviour (Wells, 1977b, 1978; Roithmair, 1994), which is related to competition for diverse limited resources such as female and oviposition, calling, and feeding sites (Wells, 1978; Martins *et al.*, 1998). On average, 70% of males of *P. rohdei* stayed in the same area in consecutive nights. In *P. rohdei*, these areas may function as courting and oviposition sites, which would explain the permanence of males in such areas and the vigorous agonistic actions of the resident males toward intruders (Wogel *et al.*, 2004).

Finally, according to Bradbury's (1981) conditions, *P. rohdei* was not considered to exhibit a lek mating system simply because females usually laid eggs at the same place where courtship took place. In other words, male territories enclosed oviposition sites.

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