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Daily Movement and Microhabitat Use by the Blacksmith Treefrog *Hypsiboas faber* (Anura: Hylidae) During the Breeding Season in a Subtemperate Forest of Southern Brazil

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Abstract. We studied the patterns of daily movement and habitat use of 20 males and five females of the blacksmith treefrog, *Hypsiboas faber*, during the breeding season in a subtemperate forest of southern Brazil. Treefrogs were tracked with externally attached thread bobbins. There were no differences between sexes in the mean straight line distance moved (HSD) or in the effective distance moved (HDM), which ranged from 0.06–3.1 m/h and 0.4–9.8 m/h, respectively). Males showed higher site fidelity and less habitat overlap than females. Despite being an arboreal species, most of the tracked individuals used the herbaceous stratum on the ground as microhabitat, which indicates a particular microhabitat use during breeding activities. Estimates of the distance moved obtained from released thread lines revealed that animals moved distances five times greater than the distances calculated by drawing a straight line between consecutive points. Therefore, our findings suggest that the sedentary behavior attributed to some tropical and subtropical anuran species in tropical and subtropical anuran species forests might not be accurate.

Keywords. Reproduction; Site fidelity; Territoriality; Thread bobbin.

INTRODUCTION

Information on spatial behavior and movement patterns is fundamental to understand habitat use and other basic life history aspects of wild populations (Woolbright, 1985; Gregory et al., 1987; Huey, 1991). Amphibians are known to have low locomotor ability and cover small distances over their lifetimes (Wells, 1977; Sinsch, 1988; Semlitsch and Bodie, 2003). Any anuran movement, including short ones, might bring key contributions to its life history, especially during a reproductive event (Bellis, 1965; Lemckert and Brassil, 2000). Most information on anuran movements refers to migration to and from aquatic breeding sites, which is the main reason for long-distance movements in amphibians (Duellman and Trueb, 1986; Forester et al., 2006). The distance covered depends on the body size, habitat, and behavior of each species and can exceed 1.5 km for mating (Kuyt, 1991; Kusano et al., 1995; Miaud et al., 2000). On the other hand, reviews about movements of breeding anurans suggest that individuals move up to a few hundred meters (Wells, 2007; Semlitsch, 2008). Accurate descriptions obtained from monitoring movements enable the interpretation of the ecological meaning of spatial habitat use. Further, adults typically migrate from breeding sites in a nonrandom manner suggesting directional movement

(Sztatecsny and Schabetsberger, 2005; Semlitsch, 2008). Constant and extensive movements, for example, may suggest an intensification of mate search or the colonization of new habitats (Breckenridge and Tester, 1961; Sinsch, 1988; Miaud et al., 2000), whereas infrequent or short movements would indicate periods of inactivity or represent an active behavior known as “site fidelity” (Crump, 1986; Pittman et al., 2008; Ringler et al., 2009). Site fidelity is the concentration of movements around a small habitat area (Tozetti et al., 2009), and such behavior has been reported for territorial calling males and species that undertake egg attendance (Crump, 1988; Donnelly, 1989; Valenzuela-Sanchez et al. 2014).

The reproductive season is the most opportune time to obtain data on the movement of anurans because numerous aspects of their social behavior are related to breeding activities (Wells, 1977; Hartmann et al., 2005; Moreira et al., 2007). During reproduction, male and female activity is limited to reproductive purposes and the decision on whether or not to move can generate direct consequences to their breeding success (Roithmair, 1992; Huckembeck et al., 2012; Iwai, 2013). In the case of species with aquatic larvae, for example, the search for specific oviposition sites by adults represents an excellent opportunity for studying the interplay between space use and reproduction. In fragmented tropical forests, many

habitat patches have no adequate reproductive sites, which forces adults to abandon forest remnants in order to reach water bodies (Haddad and Prado, 2005; Becker et al., 2007). The inability to access water bodies due to physical obstacles or to the low permeability of the matrix threatens reproductive success, especially for those species living in habitats that are spatially isolated from their breeding sites (Dunning et al., 1992). This example reveals the complexity of the decision-making process involving movements, which means that the organism should take into account frequency, duration, and direction (Crump, 1988). Consequently, increased knowledge of spatial ecology contributes to the development of effective management and conservation strategies for amphibians (Sztatecsny and Schabetsberger, 2005; Pittman et al., 2008).

The quality of the spatial data depends on the method of individual monitoring. A variety of methods have been used for studying movements of amphibians, including mark-recapture, radio-telemetry, harmonic direction finder, thread bobbins (spoon-and-line; Donnelly et al., 1994; Hodgkison and Hero, 2001; Tozetti and Toledo, 2005; Rowley and Alford, 2007), and fluorescent pounder (Graeter and Rothermel, 2007). Mark-recapture methods allow scientists to track individuals over long periods (Bellis, 1965; Donnelly, 1989; Driscoll, 1997); however, results are strongly influenced by the recapture rate, and determining multiple locations for a given individual is difficult. The selection of monitoring methods offers a trade-off between financial costs (higher for more technological apparatus) and time of monitoring (usually short in thread bobbins and shorter for fluorescent pounder). For example, thread bobbins are an effective method that avoids the underestimation of the effective distance moved by radio-tracking monitoring (Lemckert and Braszil, 2000), especially for periods of up to 24 h. In addition, some techniques are not able to be applied due to a minimum animal body size required and other attaching limitations (Richards et al., 1994). Despite the relatively short monitoring time offered by thread bobbins (up to 3 days; Tozetti and Toledo, 2005), this method has the advantage of providing data on substrate use because the thread remains attached to the vegetation, static in relation to the substrate (Tozetti and Martins, 2008; Sinsch, 1988). The thread bobbin provides information about routes and daily movements, and detailed descriptions of paths help describe behaviors of species showing a diverse reproductive behavioral repertory, as many gladiator frogs (see Martins et al., 1998).

The Blacksmith Treefrog *Hypsiboas faber* (Wied-Neuwied, 1821) is the largest treefrog in southern Brazil (8.5–10 cm snout–vent length). The species is also called as the “gladiator frog” because males actively and aggressively defend their calling and oviposition sites (Martins et al., 1998; Magnusson et al., 1999; Burger et al., 2002).

It is an arboreal, widely distributed species occurring from southern to north-eastern Brazil, as well as in Argentina and Uruguay (Kwet et al., 2010; Haddad et al., 2013). Like other gladiator frogs, males of *H. faber* construct a clay nest and maintain other males distant through the emission of advertisement calls and frequently by corporal fights (Martins and Haddad, 1988; Faivovich et al., 2005). The area that is defended around the clay nest represents either a calling site, a courtship site, or an oviposition site (Martins and Haddad, 1988). Egg attendance is facultative; hence, males may guard clutches in high-density choruses (Martins et al., 1998).

During the non-breeding season, *H. faber* is found in forests, where individuals may stay in the leaf litter (Kwet et al., 2010). During the reproductive period, however, individuals move to lentic water bodies for mating, travelling long distances between feeding sites and oviposition sites (Martins and Haddad, 1988; Colombo et al., 2008). Although nest building and parental care are well documented life history features of *H. faber*, little is known about the movement patterns of this species. The available information indicates that reproduction-related activities like nest defense and egg attendance are performed by males, a fact that leads us to believe that males should exhibit a higher degree of site fidelity than females. As such, this study aimed to assess the patterns of daily movement and habitat use by *H. faber* during the breeding season. We hypothesize that males should move shorter distances in breeding ponds and exhibit a higher degree of site fidelity than females. Further, because males defend their calling sites, we expect to find a lower overlap in the habitat use between males than between females.

MATERIALS AND METHODS

Study area

This study was performed in the Atlantic Forest domain in an area formed by a mosaic of natural grasslands associated to subtemperate forests located in the municipality of São Francisco de Paula (29°27'–29°35'S, 50°08'–50°15'W), state of Rio Grande do Sul, southern Brazil. The study site is located within the Pró-Mata Research and Nature Conservation Center (CPCN Pró-Mata), a preserved area of approximately 4,500 ha. The local climate is classified as Temperate Superhumid (Rossato, 2011), with rainfall evenly distributed throughout the year ranging from 1700–2000 mm and an annual mean temperature of 14–17°C. The local vegetation is a mosaic of Atlantic forest, Araucaria forests, and grasslands.

Individuals of *Hypsiboas faber* were monitored in two permanent ponds located within a matrix of shrubland associated with an *Araucaria* forest fragment (Fig. 1). The

mean depth of ponds was 80 cm and the vegetation cover on the water surface was 30–40% of the pond area. Aquatic vegetation was dominated by submersed and emerging small species. The two ponds are the only water bodies within a radius of 2 km and concentrate the calling activity of *H. faber* in this area (unpublished data).

Monitoring *Hypsiboas faber* movements

Sampling was carried out in January 2013 during the middle of the breeding season, which extends from December–February (Kwet et al., 2010). We monitored each pond for 2 weeks, locating calling individuals of *H. faber* by visual surveys around the ponds and capturing them by hand. We avoided capturing individuals located close to each other (< 20 m) because the tracking of movements would be biased and pilot studies showed that marked individuals released close to each other frequently

tangled their lines. Each captured individual was measured (snout–vent length; SVL), weighed, and sexed. A body condition index was estimated using the residuals of the regression of log (body mass) on log SVL (Denoël et al., 2002). Capture sites were flagged and recorded using a GPS. For each encounter, we estimated the types of microhabitat available in a virtual quadrant (1 m²) with the animal at the center. The following three categories of microhabitat were estimated: area of open water without floating vegetation, area of pond surface occupied by high vegetation (height > 50 cm), and area of pond surface occupied by low vegetation (height < 50 cm).

To obtain data on movements and microhabitat use, thread bobbin tracking devices were attached to individuals (Wilson, 1994). The bobbin consisted in a small spool of thread that unwound from the inside out. Each bobbin (produced by Hiltex Ltda.) was 2.7 g, 4 cm long, and 1.2 cm wide and contained 300 m of cotton thread. A protective case for each bobbin was made by wrapping it in a

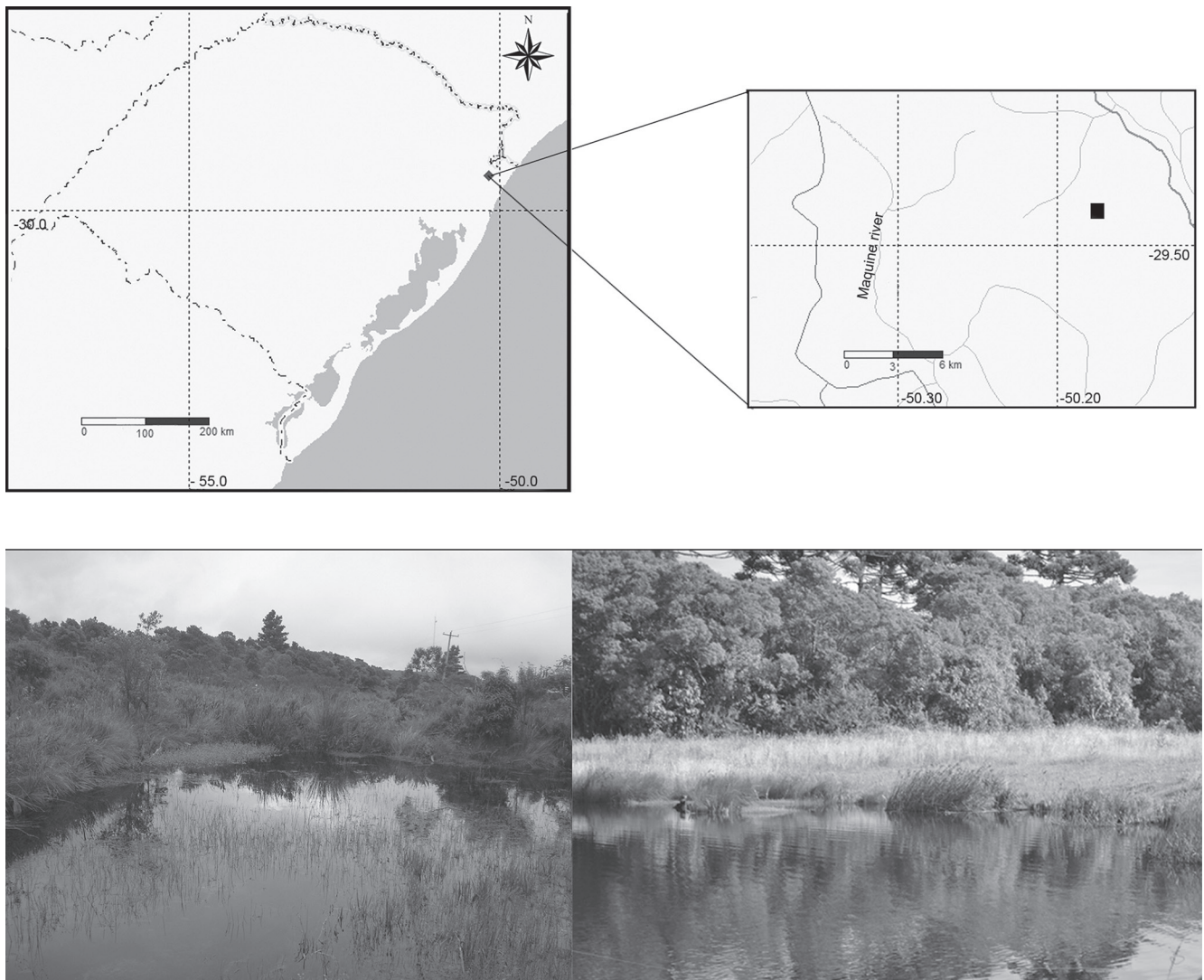


Figure 1. Localization map (dark square) and overview of the monitored ponds in the Pró-Mata Research and Nature Conservation Center, southern Brazil.

food-wrap plastic and then winding a short length of 2 cm wide adhesive tape around it. The bobbin was attached in the inguinal region of the treefrog with an elastic band belt (0.5 cm wide). The final mass of the device was approximately 3 g and was never > 10% of body mass (Richards et al., 1994).

Treefrogs were released at the capture site immediately after thread bobbin attachment. We followed thread trails twice per day: once at night (21:00–00:00 h) and once during the day (08:00–11:00 h). To prevent skin injuries, each animal was monitored for at most 2 days (Tozetti and Toledo, 2005). For each individual we measured the effective distance moved (EDM) by measuring the length of the released line, as well as the straight line distance between sequential locations (SLD; Fig. 2). Considering that the total time of tracking varied among individuals, distance was evaluated as a rate (distance moved per hour of monitoring). Thus, we estimated the mean effective distance moved per hour (HDM) and mean straight line distance moved per hour (HSD) by dividing the measured distances by the time between observations. To evaluate if treefrogs tended to remain near the initial site of marking, we calculated a site fidelity index (SF), as follows: $SF = EDM/SLD$. Higher SF values reflect a tendency of the individual to move around the initial marking site. This is a mathematical approach to evaluate the movement pattern. Continuous movement will generate higher values of EDM but the trend to move away from or remain close to the release point depends on SLD values. Circular movements for example, will generate a combination of high EDM and low SLD values (= higher

SF values). On the other hand, when both EDM and SLD are high or both are low, the metric will result in lower SF values, suggesting a trend to disperse from the release point.

Segments of EDM were classified according to substrate height as herbaceous (< 1 m) or shrub-arboreal (> 1 m). Areas representing effective breeding sites were defined using the minimum convex polygon method. We marked UTM coordinates of the outer location of the line released by each individual, so we were able to calculate a polygon area that completely enclosed all points. Due to our low number of monitored individuals, we were not able to perform a robust analysis to test for differences between sexes in habitat area. However, in addition to measuring the distance moved, we performed additional measurements to evaluate the effective moved site area (m^2) for eight treefrogs (four males and four females). To reduce the disturbance caused by our presence, these measurements were made only on one night and one day.

Data analysis

Data obtained were not distributed normally; therefore we performed a non-parametric test of variance (Mann-Whitney *U*-test) to compare differences between SF, HDM, and HSD, as well as between the sexes. The relationship between movement (HDM and HSD) and body condition was examined using a linear model regression with permutation tests (Wheeler, 2010). A paired *t*-test (one tailed) was used to compare differences between EDM and SLD, and we also compared EDM between herbaceous and shrub-arboreal strata to evaluate vertical stratification of the movements.

We used a 2-way permutational analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity to assess differences in microhabitat used between diel periods (day or night) and sexes. A non-metric multidimensional scaling (NMDS) plot was generated to visualize the spatial patterns. Data were arcsine transformed (Zar, 1998) prior to generation of the Bray-Curtis similarity matrices, which is appropriate when data are obtained from a count and expressed as decimal fractions and percentages. Analyses were conducted using the Vegan package 2.0.3 (Oksanen et al., 2012) for R (R Core Team, 2015).

RESULTS

We monitored 20 males and five females of *Hypsiboas faber* (Table 1). The mean duration of tracking (based on continuous time period over which frogs were monitored) was 17.8 ± 9.4 h (9.8–34.8 h) for males and 22.5 ± 10.3 h (11.8–33 h) for females. Animals equipped with tracking devices were observed in apparently normal behavior (e.g.,

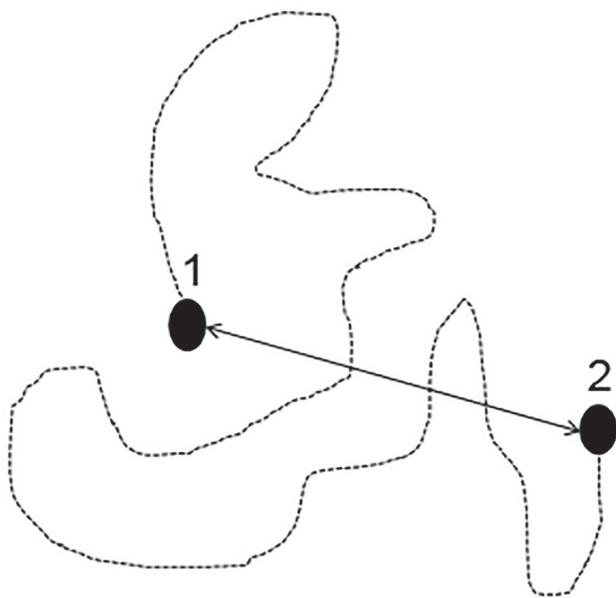


Figure 2. Model of a hypothetical movement monitored using a thread bobbin. Dashed line: released line corresponding to the effective distance moved (EDM); arrowed line: straight line distance between sequential locations (SLD).

Table 1. Morphometric characteristics and movement measurements obtained from adult male and female of the gladiator frog *Hypsiboas faber* monitored at the Pró-Mata Research and Nature Conservation Center, southern Brazil. Values are presented as mean ± SD, followed by range. SVL: snout–vent length; HSD: mean straight line distance moved per hour; HDM: mean effective distance moved per hour.

Sex	Body mass (g)	SVL (mm)	HSD (m/h)	HDM (m/h)
Female	61.8 ± 4.55 (57–69)	100 ± 5.6 (93–107)	1.2 ± 1.3 (0.12–3.1)	1.9 ± 1.5 (0.5–3.9)
Male	62.6 ± 8.64 (50–79)	94.9 ± 14.1 (40–113)	0.53 ± 0.6 (0.06–2.38)	3.2 ± 2.6 (0.4–9.8)

calling, moving through aquatic vegetation, sheltered in leaf litter and phytotelmata), which suggests that the apparatus did not affect their normal activities. Likewise, the bobbin showed no sign of inhibiting the reproductive behavior of *H. faber*, because all individuals with tracking devices were found calling and guarding clutches at varying microhabitats, and were often observed interacting

with non-marked treefrogs. During the tracking period, only one individual of *H. faber* died, encountered with predation marks at the arboreal stratum 200 m from the breeding site.

Sexes did not differ significantly in straight line distance moved per hour (HSD for males = 0.53 m/h; females = 1.17 m/h; $U = 67$, $P = 0.272$; $n = 25$; Table 1) or effective distance moved per hour (HDM for males = 3.2 m/h; females = 1.8 m/h; $U = 34$, $P = 0.303$; $n = 25$; Table 1), both of which reflect temporal aspects of movement. In contrast, the spatial aspects of movements were significantly different. Site fidelity (SF) was higher for males than for females ($U = 14$, $P = 0.01$; Fig. 3A).

The mean EDM of all tracked individuals was 4.6 times higher than the mean SLD ($t = 3.25$; $df = 24$; $P = 0.002$). However, there was no relationship between body condition and HDM ($\beta = 4.224$; $P = 0.382$) or HSD ($\beta = -0.585$; $P = 0.717$). A higher EDM was observed on the herbaceous stratum ($t = 2.75$; $df = 24$; $P = 0.005$; Fig. 3B). Only nine individuals moved on both shrub-arboreal and herbaceous strata.

Most of the diurnal retreat sites overlapped with the sites used for nocturnal activities by both sexes (Fig. 4). The PERMANOVA did not reveal any significant effect of the sex or period of the day on the type of microhabitat used (Sex: $Pseudo-F_{1,58} = 0.39$, $P = 0.634$; Period: $Pseudo-F_{1,58} = 0.93$, $P = 0.392$). At night, tracked individuals

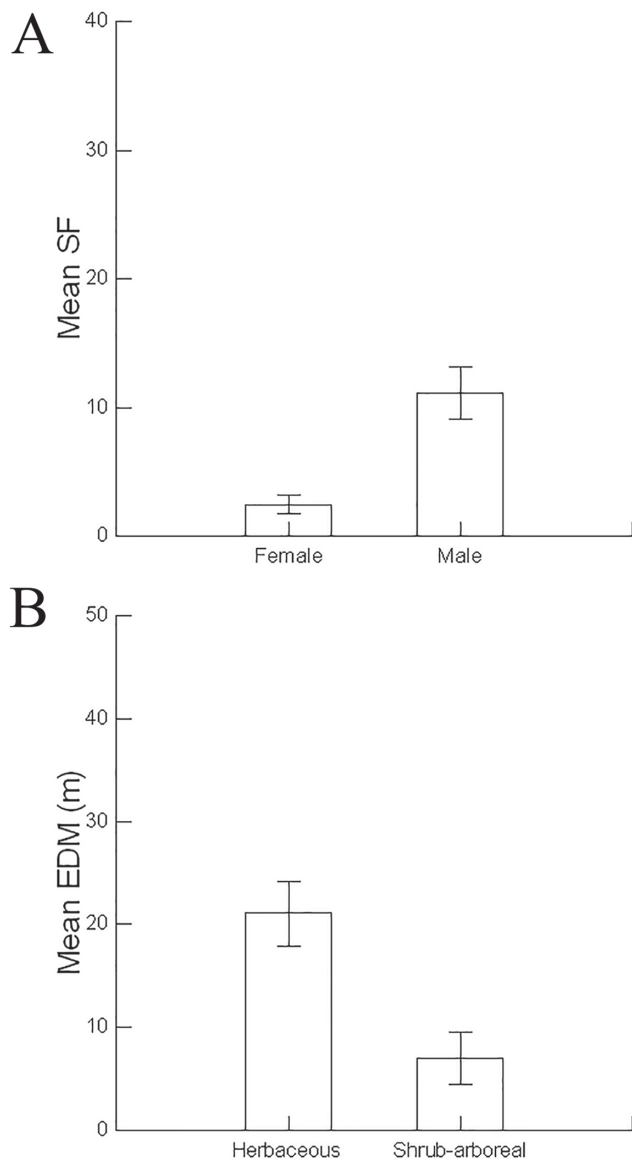


Figure 3. Results from movements of 20 males and five females of *Hypsiboas faber* in the Pró-Mata Research and Nature Conservation Center, southern Brazil. **(A)** Mean values of site fidelity (SF). **(B)** Vertical stratification of the effective distance moved (EDM). Error bars: SE.

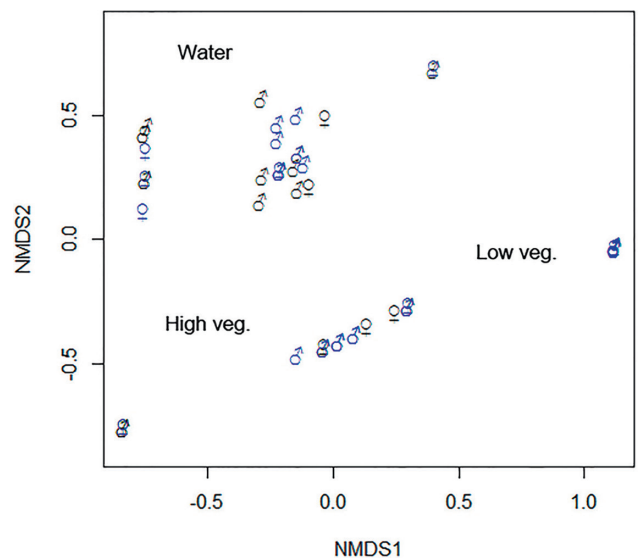


Figure 4. Non-metric multidimensional scaling plot comparing the microhabitats used by male and female *Hypsiboas faber* during the breeding season. Black symbols: nocturnal period; blue symbols: diurnal period.

were observed above water or close to clay nests. During the day, however, only four individuals moved from these microhabitats to arboreal vegetation, leaf litter, or phytotelmata. All tracked males were defending active nest sites with eggs. On average, males moved within an area of 89.8 m² and showed no overlap in breeding areas, whereas females moved within an area of 73 m² and the occupied areas of three females overlapped with the area occupied by a single male (Table 2; Fig. 5). Only two individuals moved outside the pond.

DISCUSSION

We found no difference between sexes in straight line distance per hour or effective distance moved. This lack of difference in movements between sexes is similar to the results found for some bufonids, leptodactylids, and ranids (Muths, 2003; Tozetti and Toledo, 2005; Fellers and Kleeman, 2007). Distance moved is closely related to the size of the organism, the period when the study was conducted (related to reproductive strategy, e.g., nest site defense, parental care; Iwai, 2013; Valenzuela-Sanchez et al., 2014), and sex, whereby males are likely to have smaller home ranges than females (Miaud et al., 2000; Fellers and Kleeman, 2007). A high abundance of available microhabitats generates a tendency for greater home range areas (or habitat use area), as observed in leaf litter species (see Roithmair, 1992).

Our results revealed greater site fidelity in males than females. The use of smaller areas is consistent with the territorial behavior of *Hypsiboas faber* males (Martins

Table 2. Effective moved site area tracked for eight individuals of *Hypsiboas faber* monitored in the Pró-Mata Research and Nature Conservation Center, southern Brazil.

Individual	Total moved area (m ²)	Area overlapped with conspecifics (m ²)	(%)
Male 1	63.8	23.7	37.1
Female 1	34.1		69.5
Male 2	29.2	15.8	54.1
Female 2	244.3		6.5
Male 3	8.3	4.2	50.6
Female 3	12.5		33.6
Male 4	258.2	0	0
Female 4	1.2		0
Mean			
Male	89.87	19.75	22
Female	73.02		27

et al., 1998), as also occurs in other gladiator frogs (Martins et al., 1998; Magnusson et al., 1999; Burger et al., 2002). Permanence in specific sites would favor microhabitat evaluation and improve individual ability to detect food and refuge from predators (Crump, 1988). This may be a strategy used by both sexes, as observed for the hylodid *Hylodes dactylocinus* (Narvaes and Rodrigues, 2005). The reduced overlap between male areas, in turn, could be attributed to the active, aggressive behavior of nest and calling site defense exhibit by male *Hypsiboas faber* (Martins et al., 1998), since high overlap of male home ranges indicates a low male ability in territory defense (Narvaes and Rodrigues, 2005). Intraspecific competition can lead to the defense of specific regions of individual home ranges (Duellman and Trueb, 1986; Shepard, 2002) which might be reflected in greater site fidelity. Also, although not necessarily linked to reproductive competition, the search and maintenance of oviposition sites may lead to agonistic interactions among males (Mathis et al., 1995; Pröhl and Berke, 2001; Wells, 1977, 2007). With the exception of one male, all tracked males were recaptured near their clay nests, but always outside the nests. This suggests that males might undertake some patrolling activity in the nest vicinity in order to maintain spacing between calling males, facilitate female detection, and reduce the risk of being disturbed by other males during amplexus (Martins et al., 1998; Felton et al., 2006).

The literature on amphibians states that if a species performs parental care or territorial behavior, there should be greater home range overlap in male/female comparisons than male/male comparisons (Nishikawa, 1990; Werner et al., 2010). Female territoriality has been described in amphibian species in whose females defend limited resources (e.g., refuge and feeding sites) like males do (Wells, 1977; Verrell and Brown, 1993; Mathis et al., 1995; Caldart et al., 2011; Meuche et al., 2011). Although speculative at this point, our results suggests that the habitat used by female *Hypsiboas faber* is the result of their active

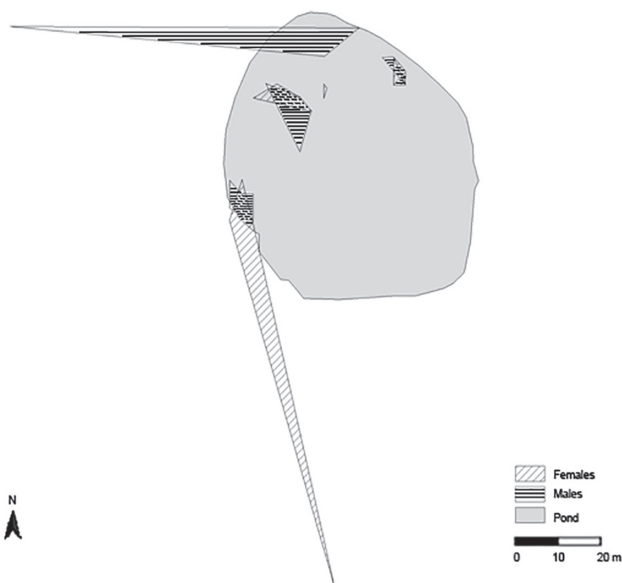


Figure 5. Diagram of a study pond showing the breeding site area of eight individuals of *Hypsiboas faber* in the Pró-Mata Research and Nature Conservation Center, southern Brazil.

search for calling males, and hence ultimately reflects the spatial distribution of males in the breeding habitats (Bastos and Haddad, 1996; Giasson and Haddad, 2007).

The absence of a relationship between movement (HDM and HSD) and body condition was expected, because we expected low variation in body condition among individuals in the breeding sites. Further, animals were tracked for a short time that was probably inadequate for significant variation to occur in individual body mass and climate variables that could affect the activities of ectothermic animals (Tozetti et al., 2010; Oliveira et al., 2013). Previous short-term studies of anuran movements have reported varying movement rates, with most individuals moving on average 50 m or less per day (Hodgkinson and Hero, 2001; Rowley and Alford, 2007); however, most studies have used linear point-to-point movement estimates (Tozetti and Toledo, 2005). Our results showed that movement analysis based on straight-line distances results in a five-fold underestimate of the effective movement of *Hypsiboas faber*. Thus, the common idea that limited daily movement is characteristic of several anuran species living in tropical and subtropical forests could be misleading (Tozetti and Toledo, 2005). The apparent distance moved may be short, but its actual movements in the intervening period are unknown. Our results using thread bobbins suggest that some commonly used methods for studying amphibian movements, such as toe-clipping and radio telemetry, might underestimate of actual daily movements and further indicate that realistic, reliable, and useful information on daily movements and microhabitat selection can be obtained by using thread bobbins. We predict that longer periods of monitoring movements will reveal key information for the conservation and management of treefrog species.

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