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Temporal Patterns of Reproductive Activity and Site Attachment of the Brilliant-Thighed Frog *Allobates femoralis* from Central Amazonia

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ABSTRACT.—Field observations and mark–recapture sampling carried out in the Reserva Ducke in Central Amazonia provided information on the occurrence of reproductive events of the Brilliant-Thighed Frog, *Allobates femoralis*, in the context of seasonal rainfall. In addition, we report on the daily pattern of calling activity and the use of space by marked individuals. Rainfall was a strong determinant of the calling and breeding activities at a seasonal scale. The phenology of *A. femoralis* was affected by interannual differences in both the length and severity of the dry season. This species showed a consistent diel pattern throughout the year, with calling activity peaking between 1500 and 1600 h. At the seasonal scale, calling activity was higher during the wet months and was correlated positively with monthly rainfall. Although recruitment is concentrated in the late wet season, our observations of juveniles in the smallest size classes throughout the year indicated that reproduction occurs sporadically even during the dry season, probably stimulated by isolated episodes of rainfall. Territories varied greatly in size, ranging from 4.8 to 175.7 m². Females did not establish or defend territories. Individuals of both sexes showed regional interseasonal attachment, and males maintained territories for up to 255 days.

Studies on temporal patterns of activity in Neotropical rain-forest frogs have focused on the seasonal responses of anuran abundance and phenology to weather determinants (e.g., Crump, 1974; Aichinger, 1987; Allmon, 1991; Gottsberger and Gruber, 2004). These observations have shown that the temporal limitation of the wet season forces species—especially those with aquatic stages—to adjust their calling and reproductive activity according to their reproductive modes. The severity of the dry season is indicated as one of the main factors affecting the time, success, and extent of the juvenile recruitment and regional permanence of individuals, therefore, determining the demographic structure of rain-forest anuran populations (e.g., Allmon, 1991; Moreira and Lima, 1991; Watling and Donnelly, 2002). Mark–recapture studies can reveal aspects of the seasonal distribution of individuals and their response to abiotic factors (e.g., Galatti, 1992; Magnusson et al., 1999), but the common restriction of fieldwork to the wet season (for dendrobatoid frogs, see a review by Pröhl, 2005) makes several studies uninformative regarding these aspects.

On the daily temporal scale, there is an extrinsic adaptive value in synchronizing behavioral and physiological processes with cyclic environmental factors (Sharma, 2003). Photoperiod and temperature cause changes in anuran activity during the course of a day (Hatano et al., 2002), whereas social facilitation affects display intensity (Brooke et al., 2000). Nevertheless, to our knowledge, no reports have quantified the diel variation in calling activity for anurans in Amazon rain forests.

The Brilliant-Thighed Frog *Allobates femoralis* (Dendrobatoidea: Aromobatidae) is a small, ground-dwelling Amazonian anuran that is a prolonged breeder where rainfall is aseasonal (Crump, 1974) and reproduces at least over the entire wet season in the central part of the biome (Gascon, 1991). Males are territorial; eggs are deposited on land; and tadpoles are carried to water on the back of the father (Roithmair, 1992, 1994). Some aspects of the complex and elaborate reproductive behavior of this relatively well-studied frog are associated with the distribution and amount of rainfall; the onset of the wet season influences the spatial organization through territory establishment by males and the occurrence of breeding events, whereas local rainfall episodes trigger parental larval transport to water

bodies (Aichinger, 1991; Roithmair, 1994; Ringler et al., 2009). Details on the reproductive behavior of *A. femoralis* in Central Amazonia are provided elsewhere (Montanarin et al., 2011). Here, we report on the occurrence of reproductive events in the context of seasonal precipitation. In addition, we describe the daily pattern of calling activity of *A. femoralis* and provide data on the use of space by marked individuals.

MATERIALS AND METHODS

This study was conducted in the Reserva Florestal Adolpho Ducke, a 10,000-ha primary terra-firme (non-flooded) rain-forest reserve near Manaus, state of Amazonas, Brazil (02°53'S, 59°58'W). The mean annual temperature is about 26°C (Marques-Filho et al., 1981), and the wet season normally lasts from November through April, with 211–300 mm mean monthly rainfall (Ribeiro and Adis, 1984). A decline in precipitation occurs during the other months, especially in August and September. However, the lengths of these seasons may vary by several months, and precipitation and soil moisture fluctuate considerably within seasons (Allmon, 1991; this study; Fig. 1). Field observations and mark–recapture sampling were carried out in a study site with an area of 9,000 m² from September 2001 to January 2003 and in a study site with an area of 125,000 m² from September 2008 to January 2010. These sites were located in the southern part of the reserve, in an area with a closed-canopy, low-light understory forest, and large numbers of stemless palms.

Individuals were located through active searching by a researcher who walked the trails that subdivided each study site. Sampling effort was distributed equally throughout the area. We visited the study sites during a total of 1,540 h to observe frogs and carry out mark–recapture sampling. This period included 870 h on 170 days from September 2001 through January 2003 and 670 h on 134 days from September 2008 through January 2010. The determination of the daily calling activity required an additional 542 h of fieldwork on 47 days from November 2001 through March 2002 and October 2008 through February 2009. The sum of the individuals recorded in spontaneous calling activity within sequential one-hour intervals from 0600 to 1800 h in the study area was used as an index of calling activity. All adult frogs captured in the study area were marked individually by toe clipping (*sensu* Hero,

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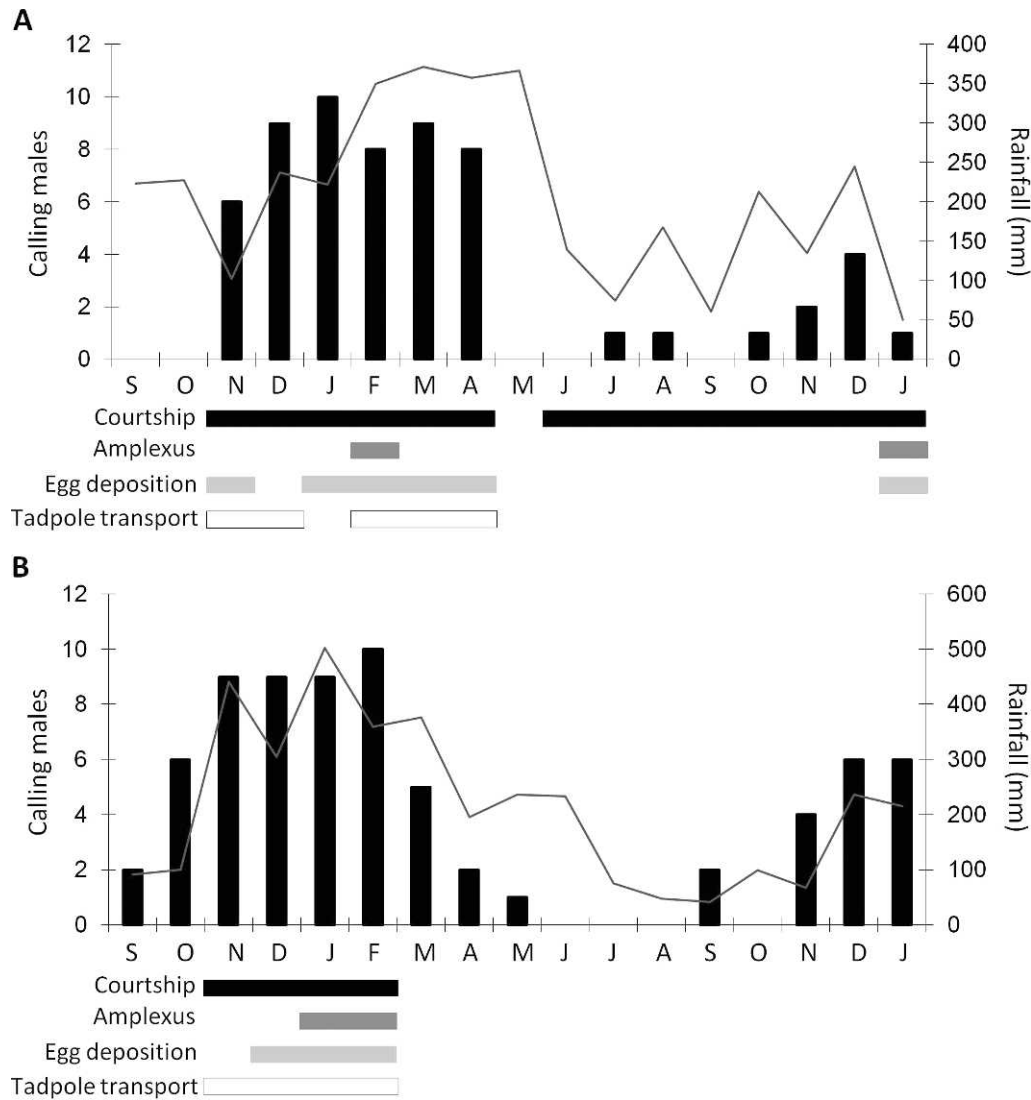


FIG. 1. Reproductive activity of *Allobates femoralis* in 2001–03 (A) and 2008–10 (B) and its relationship to local rainfall (upper line) in Central Amazonia. Months are represented in the x-axis. Vertical bars represent the number of different calling males recorded in the study area during each month. Timelines below show the occurrence of the reproductive events.

1989). In addition, juveniles were marked during the 2001–03 fieldwork period. Toe clipping was found to have no detrimental effects on recapture rates of *A. femoralis* (Ursprung et al., 2011). Also, we took digital images of the ventral patterns for comparisons and individual recognition. Frogs captured in the study area had their snout–vent length (SVL) measured to the nearest 0.1 mm and the body mass measured to the nearest 0.1 g. Frogs were sexed by the presence of the two longitudinal folds of the vocal sac of males. Individuals smaller than 27.0 mm and lacking longitudinal folds could not be sexed externally and were regarded as juveniles. During the 2008–10 fieldwork period, the locations of all individuals were marked with small numbered plastic flags attached to the ground or to the vegetation.

Territory areas (m^2) for the 2008–10 period were calculated using the minimum convex polygon (MCP) method with the animal movements extension (Hooge and Eichenlaub, 1997) in ArcView 3.2. We chose the MCP instead of the modified minimum area method (MMA; Harvey and Barbour, 1965; applied in previous studies on *A. femoralis*) because in this study capture events were rarer and more widely spaced than

reported previously for this species. Therefore, the exclusion of extreme capture points required by MMA would preclude us from estimating the size of the territory for many individuals. We defined the territory of a male as the space within the range of his call, which only he used and defended, and within which other calling males were not tolerated (Roithmair, 1992). We considered territories as only those areas where males were recorded from at least four different calling sites, all of them on different days of observation.

Monthly rainfall was measured as the total precipitation for a given month. Monthly temperature was regarded as the mean temperature for a given month. These data were recorded at the Reserva Ducke by the Departamento de Coordenação de Pesquisas em Clima e Recursos Hídricos of the Instituto Nacional de Pesquisas da Amazônia.

The distribution of data was checked for normality by applying the D'Agostino and D'Agostino-Pearson tests. Given that all the datasets showed normal distributions, correlations and differences between them were evaluated through Pearson's and Student's *t* tests, respectively. A significance level of $\alpha = 0.05$ was assumed for all analyses.

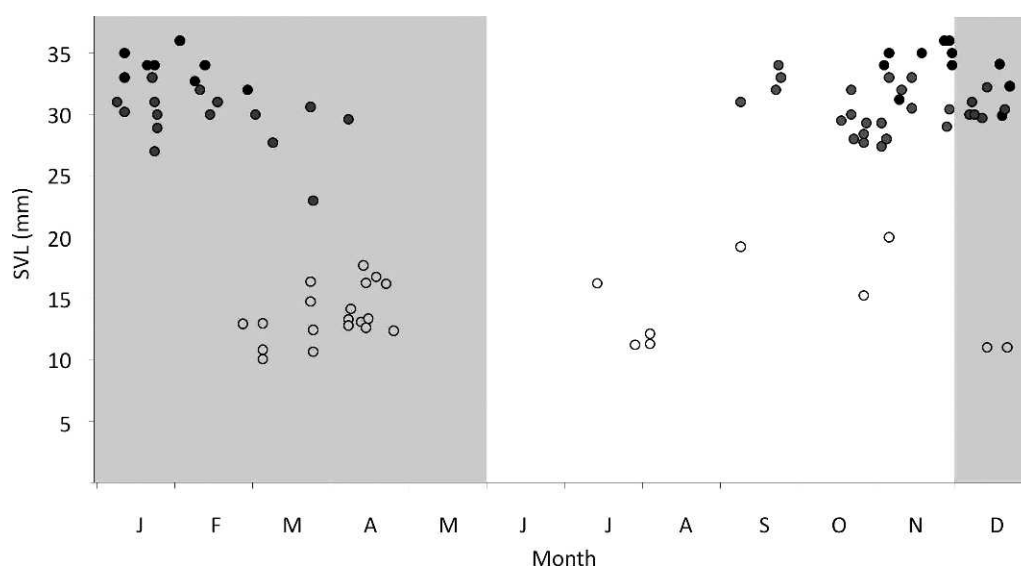


FIG. 2. Seasonal variation of the SVL of juveniles (open circles), males (gray circles), and females (black circles) of *Allobates femoralis* at the time of their first capture within the study site. The gray shading represents the rainy season. Data are displayed regardless of the year of capture.

RESULTS

We marked 28 juvenile and 67 adult (46 male, 21 female) frogs. The male:female sex ratio at the study site was 2.2:1. Juvenile SVL ranged from 10.1 to 22.9 mm (mean = 13.9; SD = 2.9; $N = 28$) (Fig. 2). Male SVL averaged 30.3 mm (SD = 1.7; range = 27.0–34.0 mm; $N = 41$); body mass averaged 2.5 g (SD = 0.4; range = 1.5–3.2 g; $N = 24$); and both were correlated ($r = 0.78$; $P < 0.001$; $N = 24$). Female SVL averaged 33.8 mm (SD = 1.6; range = 29.9–36.0 mm; $N = 19$); body mass averaged 3.5 g (SD = 0.3; range = 3.1–4.1 g; $N = 14$); and there was no correlation between them ($r = 0.22$; $P = 0.44$; $N = 14$). Females were significantly larger than males ($t = 7.55$; $P < 0.01$).

Some males and females showed regional interseasonal attachment at the study area in both fieldwork periods, although most of the individuals marked in the first wet season were not recorded again (Fig. 3). Males were recorded first and in greater numbers than females at the onset of each wet season. The first capture of juveniles was concentrated at the end of the rainy season, although new individuals were captured in the study area throughout the year. In contrast, the appearance of new adult individuals at the study site was restricted to the periods of higher precipitation.

Climate conditions and reproductive events differed both qualitatively and quantitatively within and between the fieldwork periods. Therefore, data on reproductive phenology are presented separately for 2001–03 and 2008–10. The onset and duration of the reproductive events were concentrated in the wet season and, therefore, were affected by its length and intensity. In both fieldwork periods, the beginning of the second wet season was drier than that of the first. Although amplexus, clutches, and tadpole transport were restricted to the wet season, calling activity and courtship behavior occurred during most of the year. A noticeable exception was the extended dry season of 2009, when, despite the presence of calling males, no other signs of breeding activity were recorded.

Males were found calling exclusively during daylight. Calling activity was more intense during the afternoon, peaking between 1500 and 1600 h (Fig. 4). At the seasonal scale, calling activity was greater during the wet months and was correlated

positively with monthly rainfall ($r = 0.58$; $P < 0.01$; $N = 32$ months). Monthly rainfall showed a negative correlation with temperature ($r = -0.46$; $P < 0.01$; $N = 32$ months), as did male calling activity ($r = -0.35$; $P = 0.04$; $N = 32$ months). No calling activity was recorded in some of the driest months.

Eleven territories were established within or partially within the study area, always near temporary ponds. Nine territorial males were located, two of them owners of two contiguous territories each. Territories varied greatly in size, ranging from 4.8 to 175.7 m² (mean = 65.8 m²; SD = 64.4; $N = 11$ territories). Territory size was not correlated with male SVL ($r = -0.001$; $P = 0.97$; $N = 11$) or body mass ($r = -0.07$; $P = 0.82$; $N = 11$). The length of residency varied widely: males remained from 21 to 255 days in their territories (mean = 86.3; SD = 67.5; $N = 11$ territories). Male site attachment (days of residence) was not related to territory size ($r = -0.13$; $P = 0.69$; $N = 11$). Females did not establish or defend territories.

DISCUSSION

The rain forests of Central Amazonia have no marked seasonal fluctuation in temperature or humidity, leaving rainfall as the most important abiotic factor influencing the timing and intensity of anuran reproduction (e.g., Allmon, 1991; Gascon, 1991; Moreira and Lima, 1991). As well as showing that rainfall was a strong determinant of the calling and breeding activities of *A. femoralis* at a seasonal scale, we found that the phenology of this species was affected by interannual differences in both the length and severity of the dry season. This was illustrated by both the correlation between rainfall and call intensity and the absence of records of reproductive activity during the drought that occurred in the second sampling season. Rainfall variation probably affects key resources used by *A. femoralis* and many other anuran species, such as breeding sites and prey availability (Donnelly, 1989; Hatano et al., 2002; Watling and Donnelly, 2002; Gottsberger and Gruber, 2004).

In a field study restricted to the rainy season, Gascon (1991) reported prolonged breeding activity for *A. femoralis* from Central Amazonia, extending at least from October to April. Although recruitment is concentrated in the late wet season, our

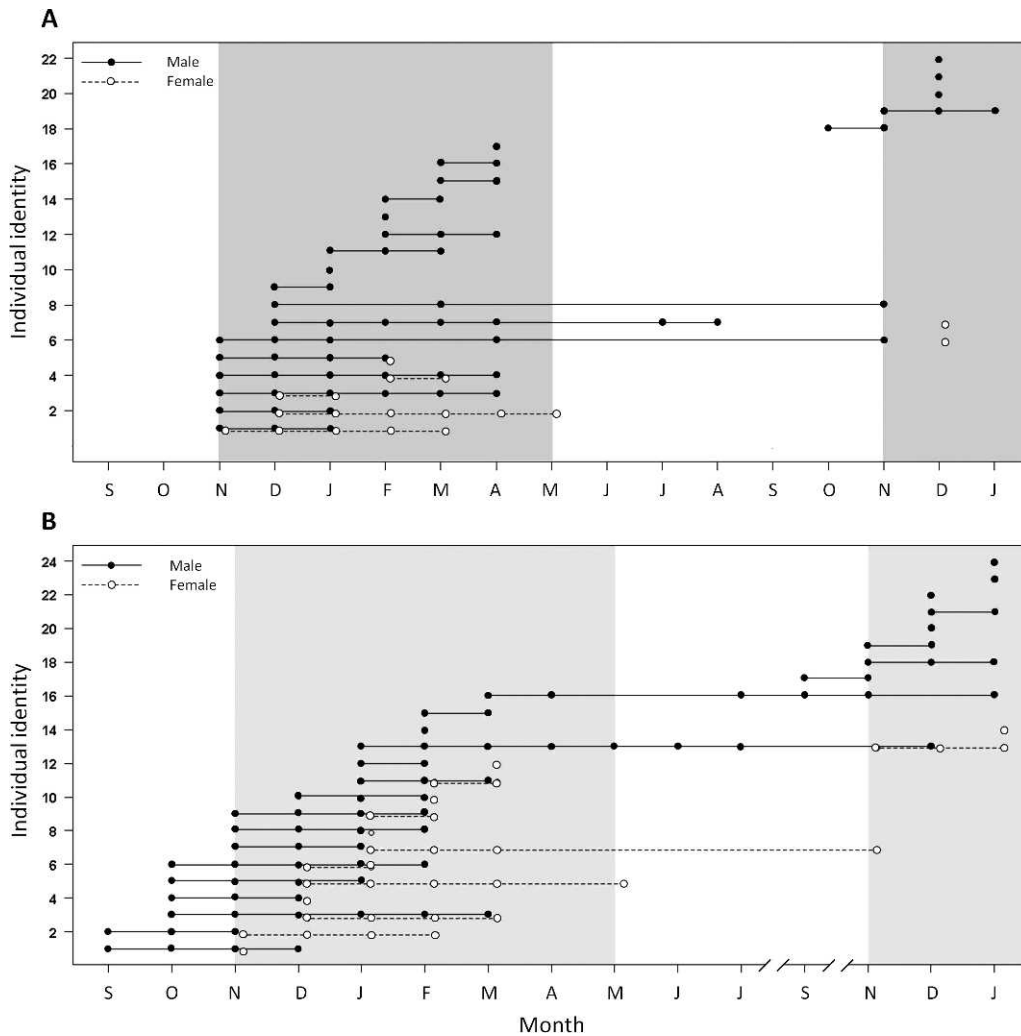


FIG. 3. Seasonal permanence of mature males and females of *Allobates femoralis* at the study sites throughout the fieldwork periods of 2001–03 (A) and 2008–10 (B). Discontinuities in B represent months with no data. The gray shading represents the rainy season. Individuals are sequentially numbered along the vertical axis according to the date of their first capture. Dots represent the capture and subsequent recaptures, and the lines represent the time elapsed between them.

observation of juveniles in the smallest size classes throughout the year indicates that reproduction occurs sporadically even during the dry season, probably stimulated by isolated episodes of rainfall. Because *A. femoralis* lays its eggs on the ground, soil moisture is sufficient to prevent desiccation (Weygoldt, 1987), whereas rainfall occurrence influences the transport of tadpoles to water bodies (Aichinger, 1991). Given that prolonged breeders may show variation in breeding intensity throughout the year (Saenz et al., 2006), we infer that reproductive activity outside the wet season took place at such a low intensity that we were unable to observe courtship, amplexus, clutches, and tadpole transport. However, the presence of juveniles during the entire dry season indicates that reproduction took place. This continuous breeding activity is commonly reported for anurans from Central American and Andean rain forests, where the dry season is not severe enough to limit the ability of terrestrially breeding anurans and recruitment data are used as an indirect measure of the length of the reproductive period (e.g., Watling and Donnelly, 2002; Valderrama-Vernaza et al., 2010).

The daily cycle of calling activity of *A. femoralis* had a first and lower peak between 0700 and 0900 h and a second and higher

peak between 1500 and 1600 h, showing a consistent diel pattern throughout the year. Anecdotal reports have previously described peaks in calling activity in the morning (0700–0900 h) and late afternoon (1500–1730 h) for *A. femoralis* in French Guiana (Hödl et al., 2004) and in Amazonian Peru (Roithmair, 1992). Roithmair reported a threefold increase in the number of calling males during the afternoon, as was demonstrated quantitatively in our study. It is known that circadian clocks confer a fitness advantage even for organisms living under constant conditions (Paranjpe and Sharma, 2005), and this might be involved in the temporal partitioning of calling activity on a daily scale.

Territories of *A. femoralis* at the Reserva Ducke (range = 4.80–175.7 m²) were larger than those reported from other localities, such as Peru (range = 0.25–26 m²; Roithmair, 1992) and French Guiana (range = 0.54–87.26 m²; Ringle et al., 2009), although there were differences in estimation methods (see Materials and Methods). Given that population density affects territorial behavior in dendrobatoid species (Pröhl, 2005), we believe that the lower density of *A. femoralis* individuals in our study site (A. Lima, pers. comm.) allows the males to establish larger

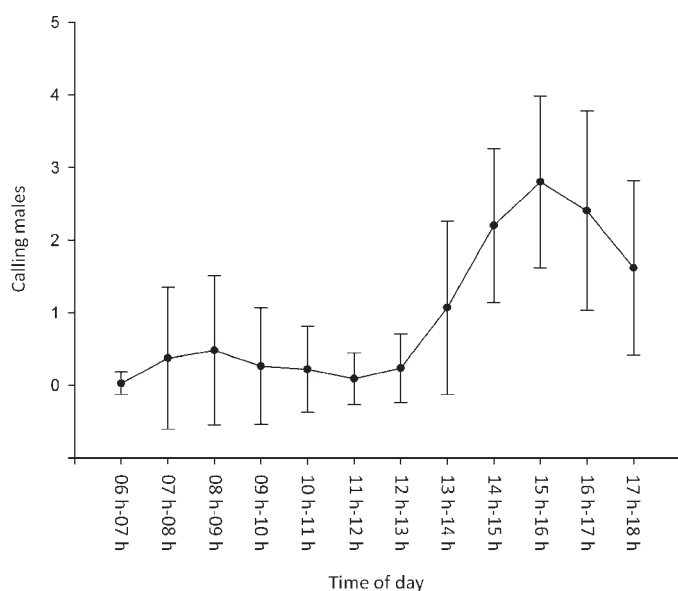


FIG. 4. Daily cycle of calling activity of *Allobates femoralis* in the Reserva Ducke, Central Amazonia. Dots represent the mean number of calling males recorded in each interval at the study site, and bars correspond to the standard deviation.

territories. Male territories were always located close to temporary ponds, which were the only water bodies available in that area. Ponds are the main extraterritorial resource and are likely to constrain the spatial behavior of male *A. femoralis* (Ringler et al., 2009). This is because males must stop defending their territories to carry tadpoles to water and then return and resume calling and territorial defense (Roithmair, 1992). Therefore, the establishment of territories near water bodies might minimize the length of absence from their calling sites, reducing the possibility of losing the territory to another male during tadpole transport.

We found that individual *A. femoralis* could survive and persist regionally from one rainy season to the next in Central Amazonia, despite the occurrence of relatively severe dry periods. Some males spent the dry season and entered the next wet season occupying the same territory. Studies of *A. femoralis* from Peru (Roithmair, 1992) and French Guyana (Ringler et al., 2009) reported a territorial residence of up to 103 and 79 days, respectively, although these authors suggested that the males might remain in their territories for much longer periods. We found males holding territories for up to 255 days. The recording of these long periods may have been made possible by our continuous tracking of individuals in the study area, including the driest period. The territories of *A. femoralis* in Central Amazonia can be classified as "Type A" according to Pröhl (2005). Such territories are related mainly to reproduction, encompassing sites for calling, courtship, oviposition, and possibly tadpole rearing. Although we do not know whether all these resources are defended actively by males of this species, all of them are located inside male territories, and this area is actively defended against conspecific calling males.

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