



The peculiar breeding biology of the Amazonian frog *Allobates subfolionidificans* (Aromobatidae)

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ABSTRACT

Allobates subfolionidificans is a vulnerable and endemic leaf-litter frog from the state of Acre, Brazilian Amazonia. We monitored a population of *A. subfolionidificans* through regular censuses and mark-recapture of 181 individuals during an entire breeding season to characterize its reproductive behavior. The space use of *A. subfolionidificans* individuals differed between sexes, with males using smaller and more segregated spaces. Males defended territories and were aggressive against same-sex individuals, which was not the case in females. The daily cycle of calling activity showed peaks in the morning and in the afternoon, and the occurrence of reproductive events was positively correlated with monthly rainfall. The breeding behavior comprised vocal and tactile interactions, although the species lacked reproductive amplexus. Egg and larvae attendance, as well as tadpole transport to water environments was performed mostly by males but occasionally by females, probably in cases of desertion by the father. This species is characterized by performing courtship, mating, oviposition, as well as egg and larvae attendance exclusively on the under surface of leaves, a unique behavior among members of the superfamily Dendrobatoidea.

Key words: Anura, Dendrobatidae, ethology, leaf-litter frog, space use.

INTRODUCTION

Discoveries on anuran reproductive behavior thrill researchers as new species are described, especially in tropical regions in the world (Crump 2015). Such findings are important not only for the characterization of the order with the greatest diversity of reproductive modes among tetrapod

vertebrates (Duellman and Trueb 1994, Haddad and Prado 2005), but also for the understanding of the evolution and conservation implications of such behaviors (Wells 2010).

Studies on the reproductive behavior of the Neotropical frog genus *Allobates* Zimmermann and Zimmermann 1988 (Aromobatidae) generally involve investigations on the maintenance of territories by males and/or females (Pröhl 2005). These areas are known to have the primary function

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associated with reproduction, being actively defended as exclusive areas necessary for complex and prolonged courtship and mating (fertilization) interactions, as well as for the defense of the offspring against desiccation, predators and cannibalism (Pröhl 2005, Wells 2010).

Species of *Allobates* are diurnal and polygamous, and territoriality is predominantly expressed by males that maintain areas in the forest floor from which they vocalize to attract females for reproduction, as well as to defend developing egg clutches prior to active transport of tadpoles to water bodies where they complete development (Lötters et al. 2007). In addition, in species such as *Allobates masniger* (Morales 2002) and *Allobates nidicola* (Caldwell and Lima 2003) eggs hatch into endotrophic tadpoles that complete development in a terrestrial nest. Reproductive modes found in *Allobates* comprise many behavioral particularities that include 1) the use of a large repertory of visual, acoustic and tactile signals during long interactions for courtship and mating such as in *A. caeruleodactylus* (Lima et al. 2002) and *A. femoralis* (Boulenger 1884) (Montanarin et al. 2011), 2) the use of different oviposition sites such as foam nests constructed by leptodactylids in *A. sumtuosus* Morales 2002 (Kok and Ernst 2007), fallen leaves on the forest floor by *A. marchesianus* (Melin 1941) (Lima and Keller 2003) and bromeliads by *A. bromelicola* (Test 1956), as well as 3) intersexual flexibility in parental care as observed in *Allobates femoralis* (e.g., Ringler et al. 2013, 2015). Many aspects of these behaviors are completely unknown for most species of dendrobatoid (Dendrobatidae + Aromobatidae) frogs, especially due to the high rate of species descriptions within the genus. Composed of 20 species prior to the 21st Century, the genus *Allobates* currently comprises 51 nominal taxa (Frost 2016).

Allobates subfolionidificans Lima et al. (2007) is a dendrobatoid species described from a single forest fragment located in Rio Branco, state of

Acre, western Brazilian Amazonia. Since its original description, the species was not recorded from additional localities, which rendered its classification as Vulnerable according to the IUCN Red List of Threatened Species (Lima 2008). Its specific epithet derives from Latin *subfolio* (under leaf) and *nidificans* (nesting) and is allusive to the reproductive site of the species, which lays its eggs on the lower surfaces of leaves. The description of the species by Lima et al. (2007) is the only publication to date that reported the use of under surfaces of leaves for reproduction by any dendrobatoid frog, and since then many details related to this behavior remained unknown. In this study, we monitored a population of *A. subfolionidificans* during an entire breeding season to analyse the spatial distribution of male and female individuals, as well as daily and seasonal vocalization patterns. In addition, we first detail the elaborate sequence of events from courtship to oviposition and subsequent care of the young by this frog species.

MATERIALS AND METHODS

STUDY SITE

This study was conducted at the type locality of *A. subfolionidificans*, an urban secondary forest fragment of approximately 100 ha (Zoobotanical Park of the Federal University of Acre; 09° 57' S, 67° 52' W) located in Rio Branco, state of Acre, Brazil. Field observations and mark-recapture sampling were performed in an 875 m² closed-canopy area located at the center of the fragment, which is drained by the small stream (*igarapé*) Dias Martins. The area consisted of a sampling grid subdivided in 25 m² subplots delimited by walking trails and sampled six days per week between 0430 and 1830 from October 2002 to May 2003 and weekly in June 2003. This sampling effort was also dedicated to a parallel investigation on the determinants of male mating success in this species (Souza JRD et al., unpublished data). Precipitation

data were obtained from the Universidade Federal do Acre meteorological station located ca. 500 m away from the study site.

BODY SIZE AND SPATIAL DISTRIBUTION OF INDIVIDUALS

Individuals captured within the study plot were sexed, measured (snout-urostyle length - SUL, in mm), and marked via toe clipping according to the system proposed by Hero (1989). Clipping of up to two toes, as performed in this study, was found to have no detrimental effects on recapture rates of *A. femoralis* (Ursprung et al. 2011). Marked individuals were immediately returned to the places of capture, which were signalized with numbered plastic flags. Males were considered residents when located vocalizing within the study plot for over one month. The size and shape of the territories of the resident males as well as home ranges of females were calculated along x and y Cartesian coordinates with the minimum convex polygon method using the program Ranges V (Kenward and Hodder 1995). The territory of a male was defined as the space used for calling activity, and within which other calling males were not tolerated (Roithmair 1992).

DAILY AND SEASONAL VOCALIZATION PATTERNS

We estimated the number of vocalizing individuals within the study plot by making censuses every hour from 0450h to 1830h once a week. A researcher walking along the trails delimiting the subplots performed counting of individuals. The characterization of the daily pattern of calling activity was based on sixteen censuses (one per week) from December to March, the period of more intense calling activity. The seasonal pattern of calling activity was characterized by weekly censuses carried out from October 2002 to June 2003.

COURTSHIP, MATING AND OVIPOSITION

Trails were silently traversed in the morning by an observer Souza JRD et al., unpublished data looking for females close to calling males. Once a potential couple was located, the sequence of events – courtship, mating interactions and oviposition – was registered at a 2 m distance using the focal animal sampling method (Altman 1974).

EGG CLUTCHES AND PARENTAL CARE

The number of egg clutches within the study site was estimated by weekly censuses, where green and dead leaves located up to 30 cm above the ground were examined. Each clutch was tagged with a numbered plastic flag and the further development was monitored every two days. We captured all individuals that carried tadpoles, measured their SUL, and calculated the number of transported larvae.

RESULTS

BODY SIZE AND SPATIAL DISTRIBUTION OF INDIVIDUALS

We captured 181 individuals: 105 males and 76 females. Most of the individuals (n=112) were marked in the first sampling month. Among the marked males, only 38.1% (n=40) were recaptured until the end of the reproductive season. Among females, this percentage was 47.3% (n=36). Male body size (SUL) varied from 15.2 to 18.1 mm (mean=16.7; SD=0.5; n=105) and female size ranged from 16.5 to 18.5 mm (mean=17.6; SD=0.5; n=76). Females were significantly larger than males (ANOVA $F_{1,179}=123.68$; $p<0.001$).

Male territories varied in size (6.0 to 40.0 m²; mean=17.7; SD=7.8; n=40) and shape (Fig. 1). The minimum distance between vocalizing males without agonistic interactions (encounter calls or physical combats) was about 1 m. Females used areas varying between 14.0 and 79.0 m²

(mean=34.0; SD=18.4; n=20) and did not engage in agonistic interactions. Male territories were smaller in size compared to areas used by females (Mann-Whitney U=666.0; $p<0.01$). We observed intersexual superposition in individual geographic ranges, and intrasexual overlapping especially among females (Fig. 1).

DAILY AND SEASONAL VOCALIZATION PATTERNS

Males started calling just before sunrise, between 0445 and 0500h. Peaks in calling activity occurred at about 0530 and 1530h. Individuals stopped calling at around 1800h (Fig. 2).

The number of vocalizing males was positively correlated with monthly rainfall (Spearman $r=0.73$; $p=0.02$) (Fig. 3). A few males were already vocally active in the beginning of our sampling in October. Calling activity remained equally high between December and March, and decreased sharply in April. One individual was found calling in May in the study area, whilst none individual was found calling in June (Fig. 3).

COURTSHIP, MATING AND OVIPOSITION

The following generalized description is based on observations of 24 *A. subfolionidificans* pairs during mating activity. Males emitted advertisement calls from leaves, twigs, trunks and roots on the forest litter. Pairs initiated a courtship march (*sensu* Montanarin et al. 2011) when females approached a calling male at a distance of 30-40 cm. Males were occasionally seen exploring leaves posteriorly used for oviposition, indicating that they evaluate structural features before conducting females to nesting sites. Males lead females to oviposition sites by emitting courtship calls, which are low-amplitude vocalizations restricted to mating contexts. Females sometimes (n=3 from 24) abandoned males during the courtship march by changing direction. In these cases, males restarted emitting advertisement calls. In two cases

this behavior recovered the females' attention and the pair resumed courtship. Pairs used green and dry leaves above the ground for oviposition. When under a leaf, the male jumped up and clung to its lower surface (Fig. 4a). He sat on the leaf with his posterior region adhered to its surface and with slightly raised forelimbs. Males emitted courtship calls from that position. A few minutes later the female jumped to the side of the male and remained with its venter adhered to the leaf (Fig. 4b). In 12 observations females attempted more than once to adhere to the leaf. In two observations females dropped out before jumping. In these two cases, leaves had trichomes on their lower surfaces and males led females to another oviposition site. Physical interactions between mating pairs were restricted to when they were adhered to the leaf. Males positioned themselves beside or behind females and touched the female's back with their forelimbs. The male climbed on the female's dorsum and touched the female's dorsolateral region with both forelimbs, one at a time, while females performed eye retraction. There was no amplexus (Fig. 4c). Immediately after, the male left the oviposition site and restarted calling. Time spent with mating interactions while adhered to the leaf ranged from 4 to 10 min (mean=6.7; SD=2.1). Courtships occurred between 0500 and 1117h and lasted from 17 to 257 min (mean=78; SD=55). Males sat at humid substrates such as phytotelmata (n=8) and wet clay (n=3) before returning to the oviposition site.

After the males' departure, females remained motionless for some minutes at the oviposition site. Subsequently, the females turned between 30 and 45° clockwise or counter-clockwise on their own axis and initiated oviposition. Eggs were laid one by one. After each egg liberation, females turned themselves and laid once again (Fig. 4d). Egg fertilization occurred without the males' presence, given that clutches removed right after oviposition developed normally (n=3). Oviposition occurred

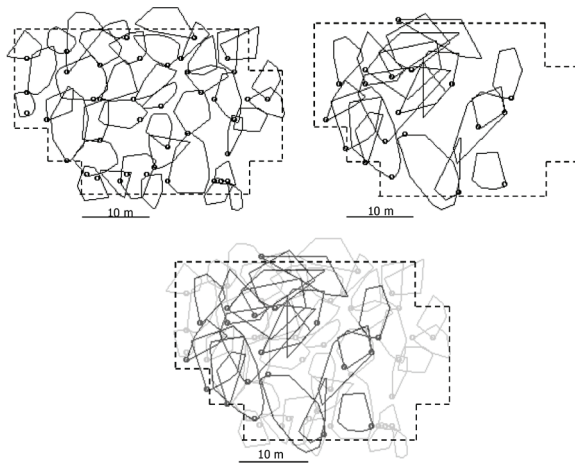


Figure 1 - Spatial distribution of male (upper panel, left, $n=40$) and female (upper panel, right, $n=20$) *Allobates subfolionidificans* individuals in the studied reproductive season in Rio Branco, Acre, Brazil. Lower panel: superposition between male territories (grey) and female home ranges (black). The dashed line indicates the limits of the sampling grid (875 m^2).

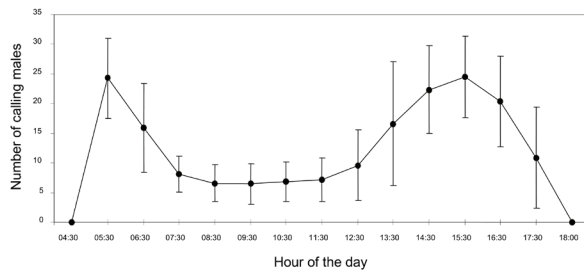


Figure 2 - Daily cycle of calling activity of *Allobates subfolionidificans* in Rio Branco, western Amazonia. Dots represent the mean number of calling males recorded in each interval at the study site, and vertical bars correspond to the standard deviation.

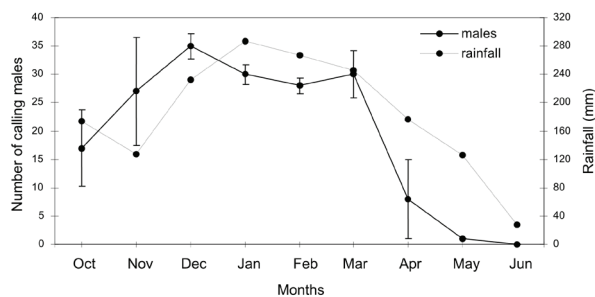


Figure 3 - Seasonal distribution of the mean number of male *Allobates subfolionidificans* in calling activity in relation to monthly precipitation from October 2002 to June 2003. Vertical bars indicate standard deviation.

between 0554 and 1122h and lasted from 5 to 13 min (mean=8.5; SD=2.2).

All males returned to the oviposition site between 38 and 242 min (mean=131; SD=54) after females' oviposition and departure. Males positioned themselves below the leaf, jumped and adhered to the leaf once again beside the clutch. Subsequently males 1) sat on the clutch and compressed the eggs against the leaf with their venter, 2) moved the eggs with their hind limbs, 3) turned around their axis ca. $15\text{-}30^\circ$ while moving the eggs. After this procedure, males abandoned the clutch. The jelly of the clutch nearly doubled in size after male's departure. The time spent by the male with the clutch varied from 20 to 37 min (mean=26; SD=3.8).

EGG CLUTCHES AND PARENTAL CARE

The first egg clutches were found in late October, and the highest production was recorded between January and February, which were the rainiest months (Fig. 5). The number of recorded egg clutches was positively correlated with monthly rainfall (Spearman $r=0.85$; $p<0.01$). Egg clutches were found from 0.5 to 23.0 cm above the ground (mean=7.3; SD=3.1; $n=760$) both in green (81.5%) and dry (18.5%) leaves. Eggs were white and the clutch size varied from 5 to 15 eggs (mean=8.2; SD=1.4).

The period between oviposition and tadpole transport ranged between 11 and 26 days (mean=16.2; SD=3.2; $n=57$). It was not possible to quantify how many times males returned to the clutch until tadpole transport. However, males returned more than once possibly to hydrate them. Males performing parental care continued to vocalize and mate females. Males mated more than once with the same female ($n=19$), took care of 1 to 5 clutches concomitantly (mean=3; $n=10$) and were not seen removing undeveloped embryos from the clutches.

The number of transported tadpoles ranged from 2 to 24 (mean=10.6; SD=7.2; n=16). There was no relationship between male body size (SUL) and number of transported tadpoles ($r^2 < 0.001$; $p = 0.945$). Only males were seen transporting tadpoles except in two occasions: 1) In January 2003 a female was captured while transporting four tadpoles; 2) In February 2003 a female was observed in the territory of a missing male visiting an egg clutch three times during a week. She performed the transport of these tadpoles to a water body after a heavy rain.

DISCUSSION

In this study, we found that areas used by males were smaller than those used by females, and only males defended territories and were aggressive against same-sex individuals. In addition, we showed that male individual ranges overlapped less than those of females. This pattern of space use is characteristic of territorial species, where spacing among males might reduce interference of other males during the complex courtship and mating interactions, as well as permitting direct access to females, oviposition sites and/or fostering the resident’s attractiveness (Wells 1977, 2010). In fact, all dendrobatoid species studied to date showed territory defense by at least one of the sexes. However, the function of a territory is variable among species of frogs and the defended resource is unknown in most of the cases (Pröhl 2005).

The daily cycle of calling activity of the studied species showed a consistent bimodal pattern throughout the year, with peaks in the morning and in the afternoon. The same pattern was quantitatively demonstrated for *A. femoralis* in Central Amazonia (Kaefer et al. 2012), thus reinforcing the notion that abiotic factors such as temperature, humidity and light intensity play a significant role in the diel variation in the emission of advertisement calls by diurnal frogs



Figure 4 - Courtship, mating and oviposition behavior of *Allobates subfolionidificans*. (a) Female on the ground before jumping and male adhered to the underside of a leaf. (b) Male and female adhered to the underside of a leaf. (c) Mating couple. (d) Female upside down performing oviposition.

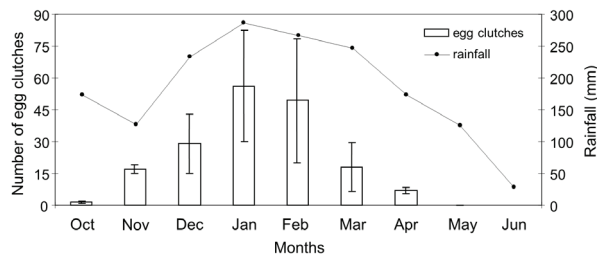


Figure 5 - Seasonal variation in monthly number of egg clutches of *Allobates subfolionidificans* and precipitation throughout the study period in Rio Branco, western Amazonia. Vertical bars represent standard deviation.

(Caldart et al. 2016). During the year, vocalization of *A. subfolionidificans* was restricted to the rainy season, as occurs in most of the *Allobates* species inhabiting Amazonian environments where seasonality is mostly determined by precipitation levels (Aichinger 1987, Allmon 1991). This is probably related to the species’ reproductive mode, which depends on ground moisture and later of temporary water bodies for egg and tadpole development, respectively. Even dendrobatoid species with endotrophic tadpoles developing entirely in terrestrial nests have their reproductive period determined by the rainy season (Juncá 1998, Tsuji-Nishikido et al. 2012), suggesting

that humidity is a limiting factor determining the reproductive period of ground-dwelling frogs.

Few investigations have provided information on egg coloration within *Allobates*, except for recent publications that have addressed this topic (e.g., Lima et al. 2002, 2014, 2015). A notably distinct characteristic of *A. subfolionidificans*' eggs is the lack of dark pigmentation, which in amphibians is related to species that protect eggs against insolation and potential predators (Duellman and Trueb 1994). This might be the case of the studied species, given that the abaxial surface of leaves might provide shelter against the deleterious effects of both sun radiation and many species of visually oriented egg predators.

The courtship, mating and oviposition behaviors of *A. subfolionidificans* are complex and involve vocal and tactile interactions, which may interact characterizing multimodal communication between and within sexes as reported for the congeneric species *Allobates femoralis* (Narins et al. 2005, Luna et al. 2010, Montanarin et al. 2011). The behavior of leaf exploration by males before oviposition was reported for the dendrobatoid *Anomaloglossus stepheni* (Martins 1989) by Juncá (1998), which proposed that males seek to optimize the courtship process to avoid female desertion. In fact, female *A. subfolionidificans* seemed to be choosy in relation to nest sites, rejecting inadequate leaves presented by males – as those extensively covered by dust and/or trichomes.

The presence of cephalic amplexus where males hold females with the upper surfaces of their front feet pressed against the females' throat during mating interactions has been observed in several species of dendrobatoid genera such as *Allobates*, *Phyllobates* and *Dendrobates* (Wells 2010). However, the absence of such behavior observed in *A. subfolionidificans* has already been reported for congeneric species such as *A. caeruleodactylus* in Central Amazonia (Lima et al. 2002) and *A. femoralis* in Peru (Roithmair 1992, 1994).

Formerly considered a dendrobatoid synapomorphy (Duellman and Trueb 1994), it is currently proposed that cephalic amplexus arose independently at least three times within the superfamily (Grant et al. 2006), although data on this topic are still inconsistent and/or not available for many species (Montanarin et al. 2011). Apparently, the tactile interaction where male *A. subfolionidificans* touches the dorsolateral region of the female body fulfils the function of stimulating oviposition, as observed in *Anomaloglossus stepheni* (Juncá and Rodrigues 2006).

Male *A. subfolionidificans* left the leaves before egg deposition and returned only after liberation of the eggs by the female, and egg fertilization occurred before the male's return. Female *A. subfolionidificans* performed eye retraction during tactile mating interactions, as noted in *Rheobates palmatus* (Werner 1899) by Lüddecke (1999). This author suggested that such behavior acts as a signal triggering sperm deposition (not necessarily internal) by the male in the female's cloacal region, which in its turn elicits the liberation of eggs.

Allobates subfolionidificans performs egg and larvae attendance, as well as transport of tadpoles from leaves to water environments mostly by males but occasionally by females, probably characterizing compensatory flexibility in cases of desertion by the father. These characteristics are shared with many other *Allobates* species with exotrophic tadpoles including *A. femoralis*, the best-studied congeneric species regarding parental care (e.g., Ringler et al. 2013, 2015). Male *A. subfolionidificans* visited egg clutches regularly, probably to hydrate them, and took concomitant care of more than one clutch. Multiple egg clutches by a single male were already observed for other species such as *A. marchesianus*, *Anomaloglossus stepheni* (Juncá 1998) and *A. caeruleodactylus* (Lima et al. 2002). However, in these species normally more than one clutch was observed on a single leaf (nest), while in *A. subfolionidificans*

the reuse of nests was rarely observed. To date, we do not have enough information to clarify whether oviposition sites are limiting resources for this and other dendrobatoid species.

Our study adds to a growing body of knowledge on the diversity of frog reproductive behavior, revealing the use of lower surfaces of leaves for calling, mating and parental care. Although common among treefrogs possessing well-developed adhesive discs at the finger and toe tips that configure an adaptation to arboreality (Wells and Schwartz 1982, Duellman et al. 2016), this behavior is surprising within Dendrobatoidea, a clade mostly composed of terrestrial, ground-dwelling inhabitants of the forest floor. As stressed by Vitt (2013), the description of behavioral phenomena comprises the observational stage of the scientific method, fundamental to construct meaningful and relevant biological hypotheses. As new species are described, research on this topic might reveal additional reproductive behaviors and allow us to understand the mechanisms behind their evolution.

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