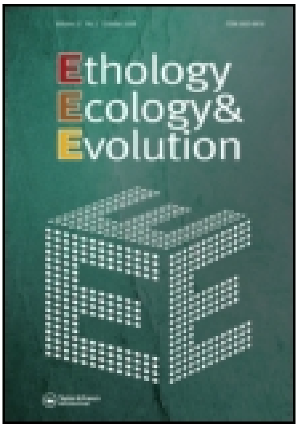

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Courtship and mating behaviour of the brilliant-thighed frog Allobates femoralis from Central Amazonia: implications for the study of a species complex

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Courtship and mating behaviour of the brilliant-thighed frog *Allobates femoralis* from Central Amazonia: implications for the study of a species complex

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The identification of divergence in reproductive traits may substantially improve integrative approaches to understand species limits within clades that are suspected to contain cryptic diversity. The frog *Allobates femoralis* has been regarded as a pan-Amazonian species, and widely used as a model for addressing evolutionary issues regarding patterns of intraspecific diversification, social organisation, and animal communication. Recent accumulation of genetic, morphological, and bioacoustic data gathered from different localities strongly supports the idea that it represents a species complex, but field behavioural observations related to courtship and mating are surprisingly scarce. Here, we provide a description of several aspects of the reproductive biology of *A. femoralis* from a Central Amazon site, and compare our results with the few published reports for the species. This study demonstrated that, besides the known divergence in the number of notes of the *A. femoralis* call, there are both quantitative and qualitative differences regarding reproductive traits between two populations of this taxon. The most striking difference was the observation of cephalic amplexus in the population from the Reserva Ducke, Brazil, which contrasts with the absence of any kind of body contact between *A. femoralis* pairs during mating interactions at the Panguana Biological Station, Peru. In addition, we report for the first time a set of visual components of the courtship behaviour, such as throat display, limb lifting, circling, and leg stretching. Behavioural differences can lead to a pre-zygotic isolation, thus representing a first step in the speciation process through differential sexual preferences. Hence, our finding of divergence in a set of traits probably related to mate recognition and choice is surprising within populations assigned to a single clade, and highlights the importance of considering behavioural traits in order to disentangle the evolutionary forces driving the diversification of *A. femoralis*.

KEY WORDS: Anura, communication, Dendrobatoidea, divergence, pre-zygotic traits.

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INTRODUCTION

Reproductive isolation, an important component of speciation models, can be generated by differences in sexual characters such as behaviours (PANHUIS et al. 2001). Given that behavioural divergence often precedes genetic differentiation (DALL 1997), comparative studies on sexual traits, especially courtship and pre-mating signals, may be particularly useful for the comprehension of stages in speciation processes that may not be readily detectable by commonly employed tools. Therefore, the identification of divergence in reproductive traits may substantially improve integrative approaches to understand species limits within clades that are suspected to contain cryptic diversity (DAYRAT 2005; WIENS 2007).

The brilliant-thighed frog *Allobates femoralis* Boulenger 1883 (Dendrobatoidea Aromobatidae) is a diurnal, ground-dwelling anuran that has been regarded as a pan-Amazonian species, and widely used as a model for addressing evolutionary issues regarding patterns of intraspecific diversification (e.g. LOUGHEED et al. 1999; SIMÕES et al. 2008; AMÉZQUITA et al. 2009), social organisation (e.g. ROITHMAIR 1992; RINGLER et al. 2009), and animal communication (e.g. NARINS et al. 2005; AMÉZQUITA et al. 2006; DE LUNA et al. 2010). The accumulation of genetic, morphological, and bioacoustic data gathered from different localities throughout the distribution of *A. femoralis* strongly supports the idea that it represents a species complex, up to eight species (GRANT et al. 2006). Species delimitation in *A. femoralis* has benefitted from integrative approaches, which have already allowed the recognition of a lineage from the western Brazilian Amazon as a distinct taxon (SIMÕES et al. 2008, 2010; AMÉZQUITA et al. 2009).

Although it is a well-studied species, when compared to other Amazonian frog taxa, information regarding the reproductive biology of *A. femoralis*, notably field behavioural observations related to courtship and mating, are surprisingly scarce. The complex and elaborate reproductive traits found in *Allobates* are recognised as useful to understand species limits within this genus (CALDWELL et al. 2002), and species descriptions in *Allobates* have been mainly based on the large data set provided by field behavioural and reproductive observations (e.g. CALDWELL & LIMA 2003; LIMA et al. 2007).

Despite its conspicuous, easily detectable advertisement call, the cryptic and prolonged courtship and mating behaviours displayed by *A. femoralis* are hardly observed in the field. The only known reports were provided for a population from the Panguana Biological Station, in Amazonian Peru (ROITHMAIR 1992, 1994). Here we provide a detailed description of several aspects of the reproductive biology of *A. femoralis* from a Central Amazon site (Reserva Ducke, Brazil), and compare our results with these reports.

METHODS

This study was conducted in the Reserva Florestal Adolpho Ducke, a 10,000 ha primary *terra-firme* rainforest reserve near Manaus, Amazonas State, Brazil (02°53′S, 59°58′W). The rainy season at Reserva Ducke lasts from December through May (211–300 mm mean monthly rainfall) (RIBEIRO & ADIS 1984) and the mean annual temperature is about 26 °C (MARQUES-FILHO et al. 1981).

Observations were concentrated on 4050 m^2 and 4950 m^2 grids in 2001–2002 and on a 150,000 m^2 grid in 2008–2009, and three courting pairs located outside these grids were also observed. The grids were located in the southern portion of the reserve in an area with a closed-canopy, low-light understorey forest, and a large quantity of stem-less palms. Adult individuals of *A. femoralis* were toe-clipped in order to ensure identification, and were monitored monthly for a study on territoriality and reproductive phenology (I.L. KAEFER et al. in prep.). Territory was defined as the calling range of a male, exclusively used and defended by him, and within which other calling males are not tolerated (ROITHMAIR 1992).

Two courting pairs were monitored in 2001–2002 and five in 2008–2009, all between November and March. Field observations were made following the *ad libitum* method (ALTMANN 1974), and each pair was observed from the moment of its location until both individuals left the oviposition site. Visual stimuli are described according to the classification proposed by HÖDL & AMÉZQUITA (2001) and HARTMANN et al. (2005), where applicable. Terminology for acoustic signals is based on ROITHMAIR (1992, 1994) and for tactile interactions follows LIMA et al. (2002) and LIMA & KELLER (2003). The number of observations after each behaviour refers to distinct individuals which have performed them, thus constituting independent observations. We compare the reproductive traits observed in this study with those reported for *A. femoralis* at the Panguana Biological Station, Amazonian Peru (ROITHMAIR 1992, 1994).

RESULTS

Pair formation, courtship, and mating: visual, acoustic, and tactile signals

Pair formation occurred as soon as a male detected the presence of a female and started to lead her to an oviposition site. Hereafter, we call the conduction performed by the male, in which he is closely followed by a female to the oviposition site, the 'courtship march'. The courtship march continued between two days for at least five pairs. Observations of these pairs in courtship started between 10:00 hr and 17:00 hr; they entered separately beneath dead leaves between 17:45 hr and 18:45 hr ($n = 4$). The pairs resumed their courtship behaviour in the first hours after daylight the following morning ($n = 5$). We observed one pair leaving the same leaves they entered individually at the beginning of the previous night. In the morning, courtship activities lasted from 50 to 210 min, until egg deposition.

Two pairs mated on the same day that they were first found courting. The first mating involved a case of female interception, described below, and the courtship interactions in this pair lasted 40 min. The second pair was observed courting for 100 min in early morning, until egg deposition.

The reproductive behaviour of *Allobates femoralis* from the Reserva Ducke was composed of visual, acoustic, and tactile signals. During the courtship march, the females repeatedly passed their arms and legs over their own bellies ($n = 5$). Males were found jumping in front of the female and guiding her through his territory (running-jumping display; $n = 7$), turning aside from the female and displaying his inflated vocal sac without vocalising (throat display; $n = 5$), performing rapid up-and-down movements of an arm or leg (limb lifting; $n = 3$), pivoting around his own axis (circling; $n = 2$), and rapidly stretching both legs at the substrate level, showing the orange patches of his thighs (leg stretching; $n = 2$).

Males emitted advertisement and courtship calls. Females oriented towards and followed males emitting both calls. Sometimes the female ceased to follow the male, and then he came back toward her and began emitting calls until she resumed walking. Courtship calls had a lower frequency and were always emitted by males at short distances (< 50 cm) from the females.

At the end of the courtship march, males either entered directly into the oviposition site ($n = 3$) or entered several sites ($n = 4$), appearing to examine them (up to six separate sites), before choosing one. During this procedure, males ($n = 2$) occasionally mounted and immediately fell from the female, without amplexing with her.

Fig. 1. — Cephalic amplexus of a pair of *A. femoralis* from Reserva Ducke, Brazilian Amazon.

Tactile displays were recorded between males and females during the last minutes of the courtship, when the pair was near or inside the oviposition site. These interactions were always initiated by the female, when she touched the snout ($n = 2$) or a side of the body of the male ($n = 4$) with her snout, or positioned the top of her head beneath his jaw ($n = 2$).

The male entered the nest, followed by the female ($n = 7$). Then she stood paired to him ($n = 5$), and after turning around, the male climbed on her dorsum while grabbing her by the head ($n = 7$). The amplexus was cephalic, which consisted of the male clasping the female with his front limbs pressed against her chin (Fig. 1). Egg deposition started at this moment. Amplexi occurred during the morning ($n = 7$), between 07:05 hr and 09:50 hr, and had a mean duration of 3.2 min (range = 2–4 min; $n = 5$). Soon after the amplexus, the male remained between 1 and 4 min (mean = 2.6 min; $n = 5$) next to the female and then left the oviposition site. Females remained 51 min (range = 32–60 min; $n = 7$) on average at the oviposition site. During their stay in the oviposition site, females constantly pivoted around their own axis over the eggs.

Clutch, fecundity, and tadpole transport

The oviposition site was always covered, given that clutches were laid between overlapping dead leaves that formed a roof over the clutch ($n = 6$) or under leaves positioned beneath a log ($n = 1$). The number of eggs per clutch (Fig. 2) ranged from 6 to 18 (mean = 13; $n = 7$). Five clutches were monitored after oviposition. The mean time of egg development until their transport as tadpoles was 19.7 days (range = 19–20 days; $n = 4$). In one clutch, the eggs were attacked by fungi and did not develop. The

Fig. 2. — Clutch of *A. femoralis* from Reserva Ducke, Brazilian Amazon.

mean number of eggs/tadpoles that developed and were transported was 53.8% (range = 0–94%; $n = 5$). All tadpoles from each clutch were carried in a single transport (mean = 8.5; range = 5–17; $n = 4$). Only males were recorded transporting tadpoles on their backs ($n = 16$).

Unsuccessful courtships

Two courting pairs stopped demonstrating interactions ca 105 min and 130 min after the beginning of our observations. The pairs were monitored until the females did not respond to male acoustic signals, and there were no further courtship marches on that day. In both cases, the female was continuously observed in the male's territory for 37 or 68 days, until they once again engaged in courtship followed by egg deposition.

Polygyny, female interception, and male–male aggression

One male courted two different females during the same day, marching alternately with one female each time. While the male was involved in courtship interactions with one of the females, the other female remained motionless on the spot where he had conducted her the previous time. We did not observe any aggressive interaction between these females. On the next morning, the male resumed his courtship behaviour with the two females, and mated with one of them. Soon after leaving the mating site, this male started emitting courtship calls, and engaged in courtship interactions with the second female. During this second courtship march, the male entered dead leaves ca eight times, apparently looking for an oviposition site, until the female was intercepted by another male, whom she began to follow to mate in an adjacent territory.

After leaving the oviposition site, the recently amplected male was approached by the first male and they engaged in physical combat for ca 15 min. After the struggle, they separated and one of the males left that site.

DISCUSSION

The pre-zygotic and mating reproductive aspects observed in this study differ from those described for *Allobates femoralis* from the Panguana Biological Station, Peru. Visual displays, tactile interactions and amplexus are reported for the first time for the population from Reserva Ducke, Brazil (see Table 1 for comparisons).

We demonstrated that, besides the known divergence in the number of notes of *A. femoralis* call (AMÉZQUITA et al. 2009), there are both quantitative and qualitative differences regarding reproductive traits between two populations of this pan-Amazonian taxon. The most striking difference was the observation of cephalic amplexus in the population from Reserva Ducke, which contrasts with the report of absence of any kind of body contact between *A. femoralis* pairs during mating interactions from the Panguana Biological Station (ROITHMAIR 1994). WEIGOLDT (1980), observing captive individuals taken from Serra do Navio, State of Amapá, Brazil, reported that mating pairs were found close together and males often sat half on top of the female. Thus, although not explicitly mentioned, cephalic amplexus may also occur in another population from Brazil.

Table 1.

Summary of the pre-zygotic and mating aspects reported in this study, compared with those described by ROITHMAIR (1992, 1994) for *Allobates femoralis* from the Panguana Biological Station, Peru.

Reproductive traits	Central Amazon	Amazonian Peru*
Advertisement call (number of notes)**	4	3
Throat display	Present	Not reported
Limb lifting	Present	Not reported
Circling	Present	Not reported
Leg stretching (colour display)	Present	Not reported
Tactile interactions	Present	Absent
Amplexus	Cephalic	Absent
Mating period	7:00 to 9:50 hr	6:05 to 6:35 hr
Courtship duration (min)	40 to 210	95 to 225
Male, time remaining at nest (min)	2.6 (1–4)	13 (7–18)
Female, time remaining at nest (min)	51 (32–60)	37.8 (18–60)

* ROITHMAIR (1992, 1994).

** According to AMÉZQUITA et al. (2009).

The evolution of the amplexus in dendrobatoids was revised by GRANT et al. (2006), who, although recognising the lack of data on cephalic amplexus for many species, found that it arose independently three times in the clade. Their analysis represents a reversal of the polarity of this character, given that cephalic amplexus was considered a synapomorphy in Dendrobatoidea (DUELLMAN & TRUEB 1986). We believe that the understanding of the evolution of this character could be greatly benefited by the acquisition of behavioural data for more species, including intraspecific variation.

Another main difference related to the reproductive behaviour of *A. femoralis* from the Reserva Ducke is the presence of a set of visual components of the courtship behaviour, such as throat display, limb lifting, circling, and leg stretching. None of these components was reported in studies conducted on the Peruvian population (ROITHMAIR 1992, 1994). They emphasised that interactions between a pair were restricted to the display of acoustic stimuli by males, followed by the female phonotactic approach. Visual and tactile displays during courtship have been widely reported for other dendrobatoid species, including members of *Allobates* (WELLS 2007). For example, the leg-stretching behaviour of males observed by us was previously reported for *Ameerega flavopicta* (COSTA et al. 2006), also in a courtship context. Both these species have bright thigh colouration, and *A. femoralis* displays geographic variation in the colour of the inguinal patch (AMÉZQUITA et al. 2009). Directional sexual selection was demonstrated to play an important role in the evolution of the aposematic colouration of the dendrobatoid *Oophaga pumilio* (MAAN & CUMMINGS 2009). Regardless of the significance of the inguinal patch for *A. femoralis* diversification, our observations, together with those by COSTA et al. (2006), provide a new context for the leg-stretching display, which was regarded by HÖDL & AMÉZQUITA (2001) as restricted to agonistic interactions.

The study of geographic variation in sexual signals is a useful approach for understanding processes of diversification. For anurans, the most conspicuous, and consequently the most employed, sexual signal to address these issues is the male advertisement call (e.g. PRÖHL et al. 2007; SIMÕES et al. 2008). However, elements related to visual and tactile displays might have paramount importance for reproductive recognition and preference, especially because they are likely to occur after the beginning of the acoustic displays, when the female is approaching a potential mate. Experimental approaches demonstrated that visual signals are important in *A. femoralis* male-male aggression contexts (NARINS et al. 2005; DE LUNA et al. 2010), and consequently visual signals are also likely to be involved in mate recognition and choice.

As observed in this study, and reported for other dendrobatoid species (e.g., SUMMERS 1992; PRÖHL & HÖDL 1999), including *A. femoralis* (ROITHMAIR 1994), females do not necessarily mate with males with whom they engaged in courtship behaviour, and unsuccessful courtships are not rare. Our observations of visual and tactile interactions during the courtship behaviour suggested that acoustic, visual, and tactile signals are involved in mate choice. Therefore, a phonotactic approach and even courtship behaviour may not provide an unambiguous assay of female mate choice in *A. femoralis* and many other dendrobatoid species.

We observed a noticeable abdomen expansion in *A. femoralis* females while the courtship interactions took place (A. MONTANARIN pers. obs.). Morphological changes in reproductive organs involving ovulation and the production of the colloid substance that surrounds and protects the eggs are known to occur during courtship interactions in the aromobatid frog *Anomaloglossus stepheni,* also leading to female abdomen expansion (JUNCÁ & RODRIGUES 2006). ROITHMAIR (1994) suggested that *A. femoralis* females from Panguana need the time during their long courtship to reach the proper physiological condition to mate, and our observations corroborate this proposition.

Our identification of a polygynous system, in which male–male aggression, but not female aggression, involves territory defence in the Reserva Ducke finds support in published reports regarding *A. femoralis* social behaviour in Peru (ROITHMAIR 1992) and French Guiana (RINGLER et al. 2009). These studies also provide data on *A. femoralis* post-zygotic traits, such as clutch size and tadpole survivorship. However, these traits are known to be strongly influenced by individual characteristics (such as body size), and local environmental conditions, respectively (DUELMANN & TRUEB 1986), which makes their interpretation difficult in an evolutionary context.

A post-zygotic trait commonly employed in evolutionary studies for this group is the tadpole transport behaviour (GRANT et al. 2006). Only males were observed transporting tadpoles in our study site. Male nurse frogs were also observed for *A. femoralis* from French Guiana (LESCURE 1976; RINGLER et al. 2009) and Amazonian Peru (AICHINGER 1991; ROITHMAIR 1994). However, eventual transport by *A. femoralis* females was reported from Rio Curuá-Una, Brazilian Amazon (one out of nine observations) (CALDWELL & DE ARAÚJO 2005) and from Ecuador and Suriname (SILVERSTONE 1976). These contrasting results suggest that biparental care may be widespread through the range of *A. femoralis*, and failure to detect nurse frogs of both sexes may be responsible for these differences. Alternatively, GRANT et al. (2006) suggested that at least some of the species within the *A. femoralis* complex may have nurse frogs of a single sex. Therefore, we highlight the importance of data description regarding this reproductive trait to better elucidate this issue.

Analyses of a partial sequence of the 16S rRNA mitochondrial gene from different localities through the range of *A. femoralis* revealed that individuals from Reserva Ducke and Panguana form a single, weakly supported clade together with *A. femoralis sensu stricto* (a sample taken 20 km from the type locality of the species, in Peru), and individuals from Iquitos (Peru), and Leticia (Colombia) (SIMÕES et al. 2010). Hence, our finding of divergence in a set of traits probably related to mate recognition and choice is surprising within a single clade, and highlights the importance of behavioural comparisons among phylogenetically distant populations of *A. femoralis*. Intraspecific divergence may reflect adaptations to local conditions during the evolutionary history (WELLS 2007). However, when reflected in behavioural traits, such differences can lead to pre-zygotic isolation, thus representing a first step in the speciation process through differential sexual preferences (PANHUIS et al. 2001). Pre-zygotic isolation through behavioural divergence meets the requirements posed by most species concepts (see COYNE & ORR 2004) to assign the status of distinct species to different populations.

We provide a first comparison regarding behavioural divergence within a single clade of a relatively well-studied Amazonian frog. Studies addressing reproductive and behavioural aspects from different localities throughout the range of *A. femoralis*, together with experimental approaches on sexual recognition and choice, should improve our understanding of the evolutionary and taxonomic significance of this divergence.

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