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Breeding biology of *Ameerega braccata* (Steindachner, 1864) (Anura: Dendrobatidae) in the Cerrado of Brazil

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Reproductive aspects of *Ameerega braccata*, a Cerrado endemic species of Dendrobatidae, were studied in the surroundings of the type locality of the species, Chapada dos Guimarães, mid-southern Mato Grosso State, Brazil. We found that males call mainly early in the morning and in the late afternoon. During courtship, the female approaches a calling male and tactile and visual communication occurs. Males call continuously while guiding females to the oviposition site, which may be situated as far as 24 m (in a straight line) from the initial encounter site. Spawn are deposited over fallen leaves on the soil surface or in burrows. Female snout–vent length and body mass did not explain the variation in ovary mass, or the variation in the number and size of post-vitellogenic oocytes. The results reported here for *A. braccata* might help to understand trends in the evolution of dendrobatids in open Cerrado environments.

Keywords: clutch size; courtship; reproduction; vocalization activity

Introduction

Reproduction within the poison frogs (family Dendrobatidae) is relatively well known for some species, and is remarkable because it includes complex displays of vocal, tactile and visual communication during courtship that have been extensively reported in the genera *Dendrobates*, *Ranitomeya* and *Oophaga* (Silverstone 1975; Wells 1977; Summers 1989, 1992; Summers et al. 1999; Summers 2000; Brown et al. 2008; Londoño and Tovar 2008; Valderrama-Vernaza et al. 2010). In the genus *Ameerega*, reproduction is well detailed only for three species: *A. flavopicta* (Toledo et al. 2004; Costa et al. 2006), *A. trivittata* (Roithmair 1994a, 1994b) and *A. silverstonei* (Myers and Daly 1979). These species use similar habitats (forest floor) for egg laying, which takes places in male territories, and they generally have complex parental care with the male carrying tadpoles on its back to a source of water. Little information on reproduction is available for other congeneric species such as *Ameerega picta*, *A. petersi* and *A. parvula* (Hödl 1990).

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Amongst Brazilian dendrobatids (26 species; Segalla et al. 2012), most (85%) are Amazonian in distribution. Only four species: *Ameerega berohoka* Vaz-Silva and Maciel, 2011, *Ameerega braccata* (Steindachner, 1864), *Ameerega flavopicta* (Lutz, 1925), and *Ameerega picta* (Bibron, 1838) occur in the savannah-like Cerrado vegetation that covers most of central and mid-western Brazil. *Ameerega braccata* was described from Chapada dos Guimarães (mid-southern Mato Grosso State, western Brazil), and is presently known from a few additional localities in the Brazilian states of Mato Grosso, Mato Grosso do Sul, and Goiás (Lötters et al. 2009).

At the type locality, males of *A. braccata* call from perches above the ground (mainly on leaves of shrubs or herbaceous plants), in open habitats (Forti et al. 2010). At the end of each calling period, males jump to the ground and begin to forage in the leaf litter (Forti et al. 2011). Information about reproduction in *A. braccata* is restricted to a single observation of a male which was carrying tadpoles on its back (Estação Ecológica da Serra das Araras) *c.*150 km west of Chapada dos Guimarães (Haddad and Martins 1994).

Herein we present data on the reproductive biology of *A. braccata* in Cerrado environments in the vicinity of the type locality of the species, with the particular objectives of: (1) estimating the diel variation in male calling activity; (2) testing whether the abundance of calling males is determined by environmental variables (temperature and air humidity); (3) assessing reproductive behaviour (how males and females interact in the reproductive habitat); (4) characterizing oviposition sites and clutch size; (5) testing whether males and females differ significantly in size; (6) determining whether male and female size is correlated in amplectant pairs; and (7) evaluating the relationship between female size and oocyte number, and size and ovary mass.

Materials and methods

Study area

Fieldwork was conducted over 96 days (from October 2007 to March 2008; in October 2008, and in December 2008) at Chácara Gaia Akaju (15°20′ S; 55°53′ W; 250 m elevation), Cuiabá, in the state of Mato Grosso, Brazil. The study site (Forti et al. 2010, 2011) is near the type locality of the species, which is in Chapada dos Guimarães. Additionally, 16 individuals were collected at the Chapada dos Guimarães National Park (15°24′ S; 55°50′ W; 650 m elevation; collecting permit SISBIO/ICMBIO 2075225).

Climate is similar in Cuiabá and Chapada dos Guimarães: semi-humid, characterized by two well-defined seasons: a cold and dry one, from April to September, and a warm and wet season, from October to March (Diniz et al. 2008). In Cuiabá, mean annual temperature is 25°C, and mean annual precipitation is 1450 mm (Schreiner et al. 2009). In Chapada dos Guimarães, mean temperature ranges from 22.8°C (in July) to 27.2°C (in October), and mean annual precipitation ranges from 1800 to 2000 mm (Pinto and Hay 2005). We studied the frogs in open habitats of Cerrado *sensu stricto* and *campo sujo*, two of the many distinct physiognomies of Cerrado vegetation (for a brief description of these physiognomies in the study area, see Forti et al. 2011).

Data collection

To estimate the diel variation in male calling activity, four censuses of 24 hours each (totalling 96 hours of observations) were conducted by three different observers, in alternate rounds. During each census, the observer walked along 600 m of an unpaved trail amidst open Cerrado habitats and recorded the number of individuals of *Ameerega braccata* calling up to 25 m away from each of the margins of the trail. Censuses occurred hourly, from 13 to 17 October 2008. At the end of each census, air temperature and air humidity were measured (to the nearest 0.1°C and 1%, respectively) with a digital thermohygrometer (Instrutherm HT-210; São Paulo, Brazil).

To assess reproductive behaviour, we made 115 hours of direct observations "sampling all occurrences" (see Altmann 1974). Observations during the morning started just before sunrise, about 4.30 am, and ended around 10.00 am, when vocalizations ceased. First, vocalizing males were located and followed; whenever a pair was formed, observations continued until the end of the courtship behaviour. Observations were made also in late afternoon, from 4.00 pm to 7.00 pm.

Interacting pairs and some additional individuals found in the field were captured, brought to the Laboratório de Herpetologia of the Universidade Federal de Mato Grosso (Cuiabá, Mato Grosso, Brazil), and euthanized following standard protocols (see Calleffo 2002). Subsequently, they were measured (snout–vent length: SVL) to the nearest 0.01 mm with a digital calliper and weighed to the nearest 0.1 g by using a spring scale.

From one of the clutches found in nature during the study, we randomly chose seven eggs and measured their diameter to the nearest 0.1 mm. In 12 females, post-vitellogenic oocytes were counted and their diameters were measured. Ovaries were weighed to the nearest 0.1 g with a digital weighing scale.

Data analysis

To examine which factors may influence frog breeding activities, we tested for correlations between climate variables (temperature and air humidity) and abundance of vocal males using the Spearman rank correlation test. This test was applied because abundance of vocal males is a scored variable, and therefore does not have a normal distribution. We compared size between the sexes to test whether there is significant sexual dimorphism using an unpaired *t*-test. To test whether the SVLs of amplectant pairs were related, a linear regression analysis was performed considering males' SVL as dependent, and females' SVL as independent variables. Size, number of post-vitellogenic oocytes and ovary mass were related to individual SVL and to body mass by using linear regression analysis. Ratios of ovary mass to female body mass, and of ovary mass to SVL were investigated through linear regression analysis, considering the hypothesis that body size is positively related to fecundity. In all statistical tests, a significance level of 0.05 was adopted. Analyses were run using Bioestat 3, Systat 12, and SAS 9.2.

Results

A total of 49 individuals of *Ameerega braccata* were captured during the study. The SVL of 37 males and 12 females ranged, respectively, from 20.3 to 25.2 mm ($X = 23.0$;

SD = 1.3) and from 23.5 to 29.1 mm ($X = 26.1$; SD = 1.4). The mean SVL of females was significantly greater than the mean SVL of males ($t = 6.63$; $p < 0.01$).

Vocalization began in early morning (usually between 4.30 and 6.00 am), and occasionally extended until 10.00 am on rainy days. Additional vocalizations were heard sporadically in the late afternoon. Abundance of calling males ($N = 96$) was negatively correlated with air temperature (rho = –0.43; $p < 0.01$), and positively correlated with air humidity (rho = 0.37; $p < 0.01$). These two climatic factors were negatively correlated (rho = −0.98; $p < 0.01$).

Males always started reproductive activities before sunrise, between 4.30 and 5.00 am, using mainly advertisement calls and displaying rapid stereotyped movements such as leg-kicking and arm-lifting. Females arrived at male territories from 5.01 to 6.40 am, and began to move around males, *c.*10 cm apart from them. At this moment, males started to emit courtship calls. As a response, a complex tactile communication was observed in five out of 16 interacting pairs: the female placed its throat on the male's head and sometimes touched the male's back with her hands. On four occasions, the female did not touch the male at the beginning of the courtship event, but used movements such as leg-kicking and arm-lifting. The courtship sequence was not observed in detail in the other seven interactions.

After the arrival of a female and initial courtship exhibition, the male started to guide her to an oviposition site. Displacement of a pair towards a supposed nest was observed on nine occasions. While following the male, the female always kept a distance of about one metre from him. At every three or four jumps, the male emitted courtship calls. Distance from the initial point to the place where the pair stopped moving and disappeared amidst leaf litter (presumably, at the oviposition site) ranged from 0.4–24 m ($N = 13$; $X = 9.64$ m; SD = 7.15 m), in a straight line, but pairs did not travel in a straight line. Whenever a male reached a supposed nest accompanied by the female, it remained there and emitted courtship calls for one to five minutes. The whole sequence (from the first encounter to nest arrival) lasted from 3 to 90 minutes ($N = 13$). Cephalic amplexus was observed on three occasions, when interacting pairs were inside supposed nests.

Eggs were deposited in shaded places, always in leaf litter, either above the ground (two occasions) or in a small, shallow burrow (a single occasion). Egg clutches were found in November 2007, and in February and October 2008. The first clutch was found opportunistically, during a search for a male. The other two were found near the place where two pairs were observed to hide under the leaves, after courtship.

Among the other 14 interacting pairs observed in the field, on five occasions the presence of observers may have caused interruption of the courtship. On two occasions, pairs were collected immediately after having arrived at the nest site. On the remaining seven occasions, males left the nest about 30 minutes after having reached it, and were followed shortly after by the female. Both soon started to forage amidst the leaf litter, in the vicinity of the nest. In all these cases, nests were inspected and no egg masses were found.

The first clutch found was composed of two egg masses at the same stage of development, with 29 and 31 eggs. The second clutch also contained two egg masses, with 18 and 20 eggs, at distinct stages of development (Figure 1). The third clutch was composed of a single mass of 27 eggs. The mean diameter of seven eggs (from the first clutch) was 5 mm, including the gelatinous capsule. The first clutch was observed twice a day for one week, after which it was collected. The second clutch completely dried

Figure 1. Two egg masses of *Ameerega braccata* found in February 2008 in an area of open Cerrado in Cuiabá, state of Mato Grosso, Brazil. Notice that the two egg masses are in different stages of development.

out after three days, possibly due to microhabitat disturbance after examination by the observer. The third clutch, adhered to the upper surface of a dead leaf, inside a small burrow in the soil, was inspected daily for 16 consecutive days. On the 17th day, about 15 tadpoles could be seen attached to the leaf.

Male SVL was independent of female SVL in copulating pairs ($N = 11$; $p > 0.05$); this may indicate a lack of size-based assortative mating. Descriptive statistics of selected reproductive data for females of *Ameerega braccata* are presented in Table 1. Surprisingly, female reproductive output was also independent of female size. That is,

Table 1. Descriptive statistics of selected reproductive data for females of *Ameerega braccata* from Cuiabá, Mato Grosso State, Brazil.

Variables	*N*	Mean	Standard deviation	Minimum	Maximum
Body mass (g)	11	1.56	0.34	1.00	2.15
Post-vitellogenic oocyte size (mm)	11	2.50	0.25	2.07	3.00
Post-vitellogenic oocyte number	11	19.09	5.86	11.00	29.00
Ovary mass (g)	11	0.05	0.02	0.02	0.09
Proportion of ovary mass in relation to body mass (%)	10	3	1.00	1.00	6.00

post-vitellogenic oocyte size, post vitellogenic oocyte number, and ovary mass were unrelated to SVL and body size in females ($N = 11$; $p > 0.05$).

Discussion

Mean values of SVL here reported for adults of *Ameerega braccata* are higher than previously known for the species ($X = 20.19$, SD = 1.32; range 18.3–21.8 mm; $N = 9$; Haddad and Martins 1994). Females were generally larger than males in our sample. Mean SVL of females being greater than the mean SVL of males has been noted, besides in *A. braccata*, in the genus *Ranitomeya* (e.g. *R. imitator*, *R. variabilis* and *R. vanzolinii*; see Caldwell and Oliveira 1999; Brown et al. 2008). Indeed, Silverstone (1975) suggested that females would be larger than males in most dendrobatids, and this pattern was also found for at least some populations of *Oophaga pumilio* (Brown et al. 2010). Monnet and Cherry (2002), studying some species of anurans, controlled for phylogeny, found that mean female–male size ratio was strongly correlated with the mean female–male age difference, an indubitable cue that age differences between breeding males and females appear to have a major influence on the extent of dimorphism. A support for this idea is that anurans display indeterminate growth and females must invest more time than males to reach an adequate body size for reproduction and for carrying eggs (Wells 2007).

Diurnal vocalization activity is widespread among dendrobatid species (Wells 1980; Hödl 1990). The bimodal peak of vocalization activity found in *A. braccata* is similar to that reported for the congeners *A. flavopicta*, from central Brazil (also an inhabitant of open habitats, similar to those occupied by *A. braccata*), *A. macero*, from Peru, and *A. parvula*, from Ecuador (Rodriguez and Myers 1993; Costa et al. 2006). The correlation herein reported between the number of vocally active males of *A. braccata* and both local air temperature and air humidity corresponds to general patterns, previously reported for other frog species (e.g. Wong et al. 2004; Costa et al. 2006; Lingnau and Bastos 2007). As reported for other dendrobatids, such as *Oophaga pumilio* (Pröhl and Hödl 1999), and *A. flavopicta* (Costa et al. 2006), pairs of *A. braccata* were always found during the morning, near male calling sites.

Dendrobatids usually display a complex courtship, which includes vocal, visual and tactile interactions (Silverstone 1975; Wells 1977; Grant et al. 2006; Wells 2007). All male–female interactions in *A. braccata* involved the initial approach of a calling male by a female, and the subsequent guidance of the female by the male, who continuously emitted courtship calls until reaching a potential nest. Leg-kicking and arm-lifting behaviours exhibited by males while emitting advertisement calls, and by females in the beginning of some courtship events, highlight red leg markings which may function as visual cues of health or reproductive condition. These behaviours are similar to those seen in *Oophaga histrionica* (Summers 1992) and *Ameerega flavopicta* (Costa et al. 2006).

Elaborate tactile displays during courtship are found in some dendrobatids, including *Dendrobates auratus*, *D. leucomelas*, *D. tinctorius*, *Phyllobates vittatus*, *Oophaga granulifera* and *O. lehmanni* (Wells 1977, 2007; Summers 1989, 1992, 2000). However, similar tactile displays were not always observed in *A. braccata*, and so tactile behaviour may not be the only cue for mating in this species. *Ameerega braccata* is similar to other dendrobatids in exhibiting cephalic amplexus (Wells 1980, 2007; Grant et al. 2006), while in some other species of the same family, such as *Hyloxalus* *azureiventris* from Peru, the reproductive amplexus is absent (Lötters et al. 2000; Grant et al. 2006). As an exception in dendrobatids, Costa et al. (2006) reported axillary amplexus in *A. flavopicta*.

Female foraging in male territories after courtship, without having oviposited, suggests that a complete courtship sequence might last more than one morning in *A. braccata*. This was reported for the aromobatid *Allobates caeruleodactylus*, in which females remain feeding and sheltering in the male's territory until the ova completely mature (Lima et al. 2002).

We cannot provide a plausible reason for pairs of *A. braccata* travelling up to 24 m from the encounter to oviposition sites. Reasons for moving such long distances must be further investigated, and this should include evaluations of the physical and biotic factors (e.g. temperature, humidity, shading, food resources and distance from suitable sites for juvenile recruitment) that influence the choice of both calling and nesting sites, as was assessed for *Ranitomeya biolat* (von May et al. 2009).

Numbers and sizes of eggs in the three clutches of *A. braccata* are similar to those found in two egg masses of *A. flavopicta* (Toledo et al. 2004) and in a clutch of *A. silverstonei* (Myers and Daly 1979). Also similar among *A. braccata* and *A. flavopicta* is the finding of two egg masses in the same nest and at the same stage of development, suggesting that males are promiscuous, with more than one female ovipositing in the same place. This idea is supported by the maximum number of 29 post-vitellogenic oocytes in the ovarian duct and of roughly twice this number of eggs in a single nest. Polygyny by males has been recorded in other dendrobatid species, such as *Ranitomeya variabilis* (Brown et al. 2008) and *Oophaga pumilio* (Pröhl and Hödl 1999), and in the aromobatid *Allobates femoralis* (Roithmair 1992). Several species of *Ranitomeya* show promiscuity in their mating system (Brown et al. 2011).

In general, larger female frogs produce more and/or larger eggs than smaller ones (Wells 2007). In *A. braccata*, statistically significant differences were detected neither between the size of individuals in a courting pair, nor between fecundity of females and their body size, probably because the sample size for this test was relatively small.

Reproductive data of *A. braccata* reported here might help to understand trends in the evolution of dendrobatids in open environments such as the Cerrado ecosystem.

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