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Samanta L. Cairo ^a, Sergio M. Zalba ^a & Carmen A. Úbeda ^b

^a GEKKO - Grupo de Estudios en Conservación y Manejo, Universidad Nacional del Sur, Bahía Blanca, Argentina

^b Departamento de Zoología, Centro Regional Bariloche, Universidad Nacional del Comahue, Bariloche, Argentina

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Reproductive pattern in the southernmost populations of South American redbelly toads

Samanta L. Cairo^{a*}, Sergio M. Zalba^a and Carmen A. Úbeda^b

^aGEKKO – Grupo de Estudios en Conservación y Manejo, Universidad Nacional del Sur, Bahía Blanca, Argentina; ^bDepartamento de Zoología, Centro Regional Bariloche, Universidad Nacional del Comahue, Bariloche, Argentina

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Anurans can be classified as explosive or prolonged breeders. In species with short breeding periods, intensive competition for females is expected. We analyse the temporal breeding pattern of *Melanophryniscus* aff. *montevidentis*, a bufonid inhabiting grasslands of Argentina, whose breeding is concentrated in events of short duration. Males are active during more than one breeding event per season, whereas most females take part in a single event per season. Active males outnumbered females by up to 14 times at one event, operational sex ratio (OSR) ranged from 0.07 to 0.75 and intensity of sexual selection (I_s) from 0.69 to 24. We found a negative association between I_s and OSR, but no correlation between number of active males per event and OSR or I_s . The OSR is the key that regulates the intensity of sexual selection, nevertheless, and in spite of being explosive breeders, females would potentially have chances to select their mate.

Keywords: explosive breeding; operational sex ratio; *Melanophryniscus*; Pampean grasslands; Argentina

Introduction

Many anuran species congregate at specific sites and times to breed, forming groups made up of a few to many individuals. The duration of the breeding events may vary according to the species, ranging from a single night per year to the entire year (Duellman and Trueb 1994). Wells (1977) classifies anurans into two categories according to the duration of their breeding events: explosive breeders, with breeding periods lasting a few days to a few weeks, and prolonged breeders, with breeding periods lasting over a month. Although this classification may be considered artificial, because the duration of breeding events is a continuous variable, its implications are interesting from the standpoint of sexual selection and competition. In species that concentrate their breeding activity in short periods, competition among males for females is expected to be more significant than female choice, because of the high level of synchrony among the breeders, which tends to result in dense aggregations at breeding sites. In contrast, for prolonged breeders, female choice of males is more relevant because of the asynchronous arrival of the females at breeding sites (Wells 1977).

Beyond any classification, the timing patterns of anuran breeding are usually highly plastic and may vary in time and space among populations of the same species

*Corresponding author. Email: scairo@criba.edu.ar

(e.g. Miaud et al. 2000) and even within the same population (e.g. Sullivan 1986). These variations found in breeding patterns are closely related to abiotic factors such as precipitation and temperature, and biotic factors, including competition and predation (Wells 2007).

The intensity of competition among individuals of the same sex and the chances of selecting a mate at each breeding event depend on the operational sex ratio (OSR, e.g. Tejado 1988; Lodé et al. 2005), which is the average ratio of fertilizable females to sexually active males at any given time. This ratio is strongly affected by the degree of spatial and temporal clumping of the limiting sex (Emlen and Oring 1977). The more biased the OSR is towards one sex or the other, the stronger the competition will be within the sex that is in excess (Kvarnemo and Ahnesjö 2002). According to Kluge (1981), the intensity of sexual selection (I_s) is usually high in explosive breeders as a result of the excess males at each breeding event. Wells (2007) mentions that in explosive aggregations, males usually outnumber females at any given event as well as throughout the breeding period. This imbalance leads to fewer than 5% of the males mating more than once per season, and some do not manage to mate at all.

Many bufonid species from temperate regions breed explosively during the warm months, using temporary environments (Duellman and Trueb 1994). This is true for the southernmost populations of South American redbelly toads, *Melanophryniscus* aff. *montevidensis*, which inhabit temperate grasslands in the transition between the Argentine Pampas and Patagonia (Cairo 2010). They breed in temporary ponds from October to March (Cairo et al. 2008). Each breeding event is triggered by precipitation >35 mm, and pairs in amplexus are observed for 1–5 days after the rain begins (Cairo 2010).

In this paper we analyse the temporal breeding pattern of *M. aff. montevidensis*. The concentration of breeding events in a few days is characteristic of a typical explosive breeder (*sensu* Wells 1977). We suggest the following hypotheses regarding the breeding behaviour of this species: (1) there is a marked imbalance in the proportion of sexes at each breeding event, with a male-biased OSR; (2) there are high levels of I_s ; and (3) a high proportion of males do not mate during each breeding season. To test these hypotheses we studied the frequency of individual male and female participation in breeding events over four consecutive breeding seasons, determined OSR and I_s and analysed their variations between breeding events.

Material and methods

Study area

The study area is located at Ernesto Tornquist Provincial Park (38°03' S, 62°02' W) in the Ventania Hills (Buenos Aires, Argentina) (Figure 1). The park covers 6718 ha of foothill valleys and mountains, ranging from 450 to 1186 m above sea level, and is considered one of the last remnants of Pampean grasslands (Fiori et al. 1997; Bilenca and Miñarro 2004). The Ventania Hills are of special geological, biological and ecological interest. Kristensen and Frangi (1995) refer to them as an “orographic island”, which has allowed the preservation of evidence of various events of the past. The environmental heterogeneity of the hills enables the existence of great biological diversity, and they are a veritable refuge for species with a variety of ecological requirements (Frangi and Bottino 1995).



Figure 1. Location of Ernesto Tornquist Provincial Park ($38^{\circ}03' S$, $62^{\circ}02' W$) in Buenos Aires Province, Argentina.

The climate is temperate with well-defined summers and winters, and mild springs and autumns. Mean annual temperature ranges from 14 to 20°C . Temperature can exceed 40°C in the hot season, whereas winters are cold, with absolute minimum records as low as -10°C , and occasional snowfall. Mean annual rainfall is 380 – 842 mm, especially concentrated in the austral spring and summer (September to February). Soil humidity is exhausted from October to November and the water deficit lasts until the following April (Campo et al. 2004).

Our data came from a set of stream pools resulting from the drainage of an intermittent stream that runs between sharp rocky cliffs. Eight ponds where toads usually breed were identified with numbers increasing according to their position upstream along a 230-m transect.

Sampling

Melanophryniscus aff. *montevideensis* breeding activity was monitored for four breeding seasons, from February 2006 to March 2009. Ponds were surveyed immediately after rains exceeding 35 mm, in search of active individuals, completing a total 16 sampling events (96 hours of total sampling effort). All the individuals detected at the breeding sites during reproductive events were considered as being active, and recorded. Toads were sexed, photographed with a digital 8.0-Mp camera, and assigned to the different ponds and dates. Ventral and dorsal colour patterns in this species vary from toad to toad and can be used as unequivocal marks for individual identification (Cairo and Zalba 2007). This allowed us to identify and catalogue individual toads for further analysis. Identifying individuals by means of successive photographs does not affect them (Heyer et al. 1994) and avoids the use of other more intrusive techniques, such as toe clipping, tattooing, heat branding, freeze branding, ringing or painting with fluorescent pigments. The photographs taken during the 4 years of sampling were analysed visually to detect repeated records of the same individual.

The active male : female ratio was calculated for each breeding event and each breeding season for the total ponds sampled.

The number of recaptures per individual and number of individuals taking part in amplexus were counted for each sex during the four breeding seasons. The number of times each individual mated per season and the percentage of individuals that took part in more than one amplexus per season were calculated. In addition, it was evaluated whether the females recaptured in amplexus were mating again with the same males.

We determined how many individuals were active at more than one breeding event per season, how many were only active once per season and how many skipped a season and reappeared the following season.

A correlation analysis (Zar 1999) was used to test whether the number of females was related to the number of males during reproductive events. For each breeding event, OSR was calculated as number of fertilizable females/number of males ready to mate (Emlen and Oring 1977), while intensity of sexual selection (I_s) was defined as:

$$I_s = \sigma^2 / \bar{x}^2$$

where σ^2 is the variance of the number of mates per male and \bar{x} is the average number of mates per male (Wade and Arnold 1980). Lastly, correlations were performed between (1) OSR and the number of active males, (2) I_s and the number of active males, and (3) I_s and OSR.

Results

Over the four breeding seasons studied, 84 individual males and 60 individual females were identified. Total active males outnumbered females by up to 14 times at a single breeding event, whereas the active male : female ratio per season ranged from 2 : 1 to 7 : 1 for total ponds.

Forty-nine males (58% of the total) were recaptured one to six times over the entire sampling period. Seventeen of the recaptured males were never found in amplexus, 18 were found once in amplexus, 12 twice and two on three occasions.

Considering the total individual males that were identified across this study, 46% were never found in amplexus, 48% took part in amplexus but only once per season, and only 6% were found twice in amplexus in the same season (Figure 2A).

Fourteen females (23% of the total) were recaptured one to three times over the four breeding seasons studied. All the recaptured females were captured at least once in amplexus. Three of them were seen in amplexus once, six twice and five on three occasions.

Of the total number of captured females, 22% were not detected taking part in amplexus, 77% were detected at least once in amplexus but never in more than one amplexus per season, and only one female mated twice during the same breeding period (Figure 2B). No female recaptured in amplexus was found with the same male.

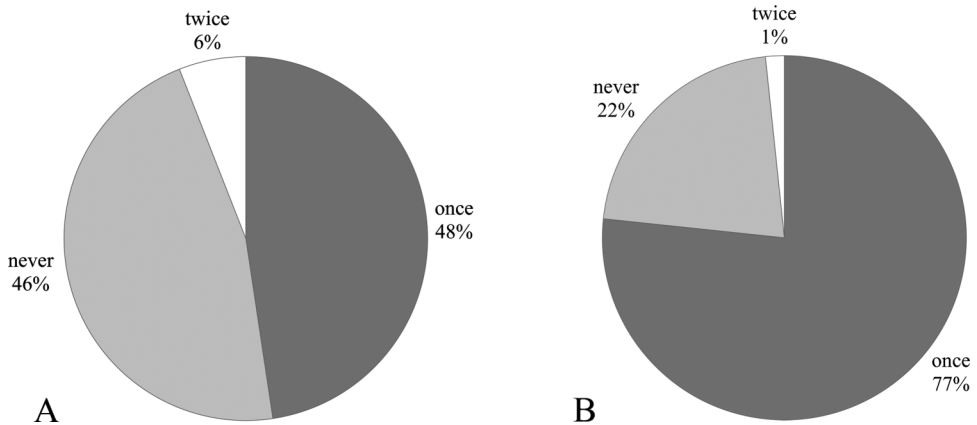


Figure 2. Percentage of *Melanophryniscus* aff. *montevidensis* toads found in amplexus (never, once, twice) per breeding season at Ernesto Tornquist Provincial Park: (A) males, (B) females.

Males were found to be active at more than one breeding event per season, usually every season. Of a total 113 re-observations of males, 52 (46%) were during the same breeding season, 54 (48%) during the following season and only seven re-observations (6%) were made two seasons after the initial capture, without having been observed during the period in between. For females, most were found to take part in a single breeding event each season, but were found to be active season after season. Of a total of 21 re-observations of females, only two were recaptured during the same season, but only one of them was found in amplexus both times. Eighteen re-observations (86%) were made in successive seasons and only one female skipped a breeding season (Figure 3).

The number of active females increased significantly with the number of males ($p < 0.01$; $r = 0.85$; $n = 16$ breeding events). The OSR ranged from 0.07 to 0.75 while the I_s calculated for each breeding event ranged from 0.69 to 24. No significant association was found between OSR and the number of active males during the 16 breeding events ($p = 0.53$) or between I_s and the number of active males during the 10 events when amplexus was recorded ($p = 0.83$). However, a significant negative association was found between I_s and OSR ($p = 0.01$; $r = -0.75$; $n = 10$ reproductive events; Figure 4).

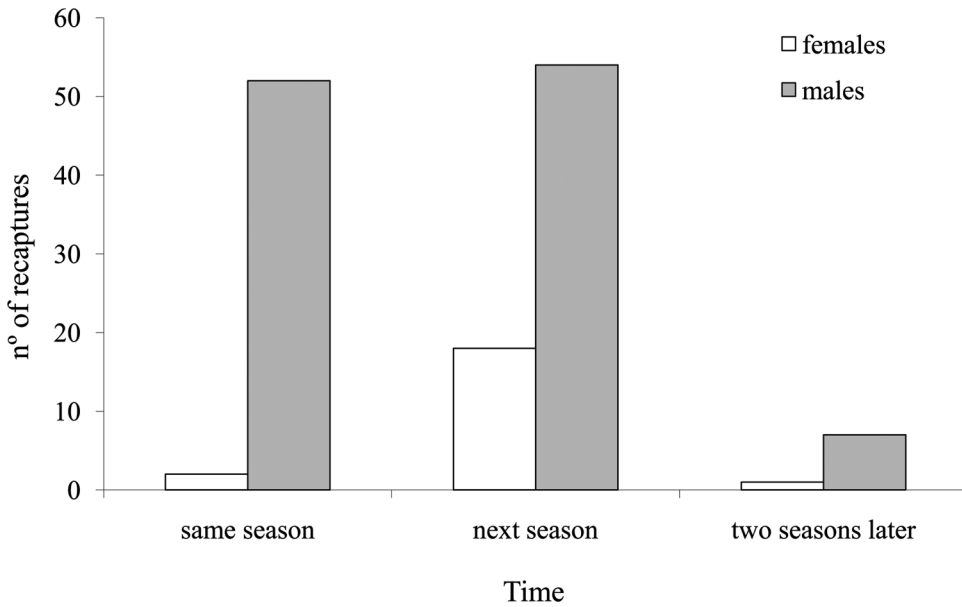


Figure 3. Number of female (white columns) and male (grey columns) recaptures for *Melanophryniscus* aff. *montevidensis* in breeding ponds associated with a temporary stream at Ernesto Tornquist Provincial Park during breeding seasons from 2006 to 2009.

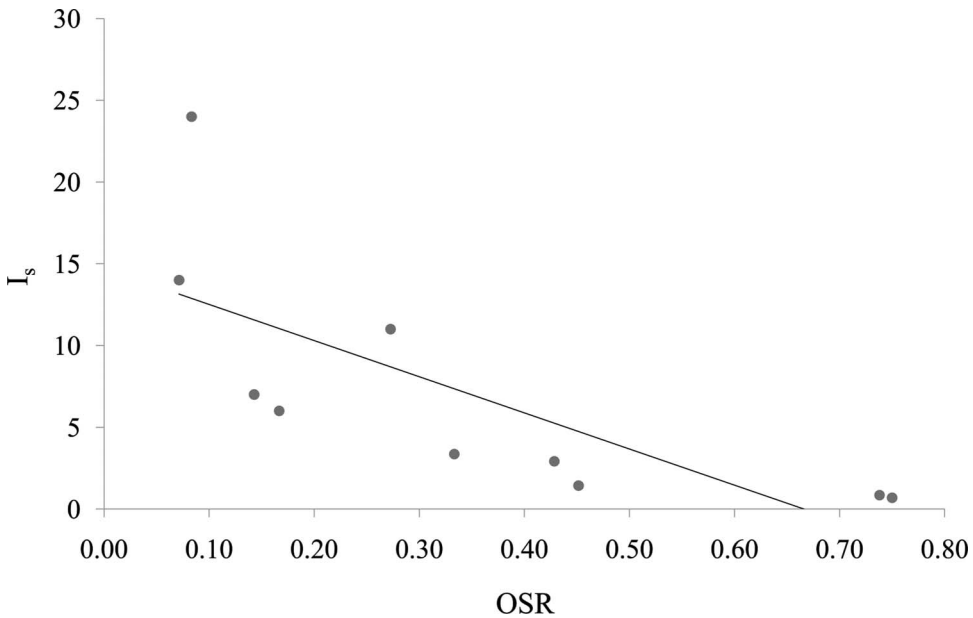


Figure 4. Relationship between the operational sex ratio (OSR) and the intensity of sexual selection (I_s) in *Melanophryniscus* aff. *montevidensis* breeding in ponds associated with a temporary stream in Ernesto Tornquist Provincial Park during breeding seasons from 2006 to 2009.

Discussion

The study of temporal breeding patterns is important for determining how the individuals of different sexes interact and how they distribute their energy during breeding, thus contributing to the understanding of population dynamics in anurans. South American species are under-represented among studies with this scope and this paper is the first contribution to the understanding of the temporal pattern of reproduction of amphibian species in the South American Pampas Biome.

According to its breeding pattern, *M. aff. montevidensis* can be considered an explosive breeder, with dense aggregations of individuals at breeding sites. Males outnumbered females at all breeding events. Many males (46%) never mated, a few (6%) took part twice in amplexus in a single season and no male had more than two mates in a single breeding season. These values are very close to those reported for explosive breeders (Wells, 2007).

Females took part in a single breeding event per season, in agreement with reports for other amphibian species in temperate zones, which usually lay eggs once a year (Lofts 1984; Sinsch 1988). Nevertheless, different females can be found breeding throughout the whole reproductive season, from October to March. In this sense they could be considered similar to prolonged breeders, in which females arrive at the breeding sites asynchronously. However, due to the short duration of each reproductive event in *M. aff. montevidensis* it seems more reasonable to analyse each breeding event independently. From this standpoint, females are available at the breeding sites for a short period of time, and necessarily must find a mate quickly, which is typical of explosive breeders (Wells 1977).

In contrast to females, a large percentage of males return to the breeding habitat more than once per season. This difference in within-season breeding frequency found between males and females may be related to the way in which each sex invests its energy in breeding. According to McCauley et al. (2000) the energy budget for reproduction is a major influence on anuran breeding patterns, with the cost of sperm production being much lower than that for oocytes (Wells 2007). In agreement with the claim made by Trivers (1972), male breeding success in *M. aff. montevidensis* could be determined by the number of mates they are able to acquire, while female breeding success could be determined by the amount of energy available for producing oocytes. This would lead males to participate in multiple breeding events and females to participate in a single breeding event.

This study showed that the number of breeding females increases with the abundance of males ready to mate in agreement with studies on a number of different anuran species (Ryan et al. 1981; Wagner and Sullivan 1992; Bastos and Haddad 1996; Rico et al. 2004; Alcantara et al. 2007). Lucas et al. (1996) claim that typically, a positive relationship between the number of females and males attending choruses is presumed to result from the use of common environmental clues by the sexes. For *M. aff. montevidensis* the volume of rainfall is the clue that triggers the start of breeding; individuals of both sexes appear to be able to detect differences in the volume of rainfall and so respond to the intensity of this stimulus with variations in their relative abundance (Cairo 2010). The hypothesis that the two sexes respond to the same environmental variables was tested experimentally by Murphy (2003), who proposed that the correlations between the number of males and females are not the result of assessment by either sex of the numbers of individuals of the

opposite sex. Furthermore, the fact that we did not find any relationship between OSR and the number of males present could indicate that females do not have preferences for large choruses, as reported for other species (e.g. Alcantara et al. 2007).

The OSR calculated in this study was highly variable between breeding events, as can be seen in Figure 4. The proportion of sexes was usually highly male-biased, although on certain occasions, the number of females was close to the number of active males. Following Wells (2007), these variations in OSR complicate any prediction regarding the sexual selection operating in the populations. However, it is known that an increase in the breeding rate of males, i.e. an increase in the average number of breeding attempts per male per season, leads to a male-biased OSR and an increase in competition for available females (Sullivan et al. 1995). Kluge (1981) suggests that in anurans with short breeding periods, large deviations in the sex ratio in favour of males result in high values for I_s . Our study supports this claim with the results of the negative correlation found between OSR and I_s . High I_s values were associated with low OSR values, i.e. events in which the sex ratio was highly male-biased. Other studies of bufonid species with short breeding periods also showed that the intensity of sexual selection correlates with the operative sex ratio (Wells 2007).

The range of intensity of sexual selection calculated for *M. aff. montevidensis* was very high, even higher than the 1.59–15.63 reported by Sullivan (1986) as surprising for *Bufo woodhousei*. However, in contrast to Sullivan's results, in our study I_s was not correlated to the number of active males. It is therefore clear that the operational sex ratio is the key that regulates the intensity of selection in this population. Hence, there is an interesting paradox in that females of this species would potentially have good chances of selecting a mate, despite being explosive breeders.

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