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Breeding-site selection by red-belly toads, *Melanophryniscus stelzneri* (Anura: Bufonidae), in Sierras of Córdoba, Argentina

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Abstract. Differences among wetlands can have important consequences on reproductive success of amphibians; therefore habitat selection is expected to be of particular importance for anurans inhabiting heterogeneous environments. To investigate if the red-belly toad (*Melanophryniscus stelzneri*; Anura: Bufonidae) uses available habitats differentially and to determine the main factors influencing the use of certain water bodies as breeding habitat, we surveyed 30 spawning sites used by red-belly toads, and 30 adjacent unused sites, in an area of the Sierras of Córdoba, Argentina. We evaluated the relative importance of morphological and biotic features of ponds, and the presence of other organisms within the water body on the use of ponds as breeding sites by red-belly toads. Eight habitat variables related to important water body features were recorded and were used to fit a habitat selection model with GLM. Red-belly toads presented a positive selection to *mallines*, a wetland characteristic of the Sierras of Córdoba. They were associated with small, shallow ephemeral ponds with muddy banks and a high percent of vegetation cover. In general, the ponds used did not host other anuran species or potential predators. Breeding site selection by red-belly toads is largely consistent with records for other species of the genus in other parts of Argentina.

Keywords: anuran, endemic species, habitat selection, reproduction, temporary ponds.

Introduction

Choice of oviposition site plays an important role in the reproductive success of temporary pond amphibians (Resetarits and Wilbur, 1989). Many anurans, particularly in temperate regions, require aquatic environments for successful reproduction. Yet, the diversity of aquatic habitats in which anurans specialize suggests that water bodies are not equally suitable (Resetarits, 1996). In many organisms, offspring may be unable to leave the sites selected by their parents if conditions become adverse (e.g., larvae in temporary-pond breeding amphibians). Therefore, the choice of oviposition site can directly influence fitness by establishing the conditions for larval development (Resetarits and Wilbur, 1989). Considering the large differences among breeding ponds and their consequences on reproductive success, there should be a strong selective pressure on the ability of breeding individuals to discriminate between high- and low-quality breeding sites (Murphy, 2003; Rudolf and Rödel, 2005); also, habitat selection should be particularly important for anurans inhabiting heterogeneous environments highly susceptible to changing biotic and abiotic factors (Orians and Wittenberger, 1991; Haramura, 2007).

Active selection of breeding sites in response to abiotic characteristics, such as pond depth, water temperature and vegetation cover, and biotic factors, such as the presence of predators and competitors, has been frequently documented (e.g., Crump, 1991; Vos and Chardon, 1998; Blaustein, 1999; Skelly, Werner and Cortwright, 1999; Skelly, 2001; Hazell et al., 2003; Goldberg, Quinzio and Vaira, 2006).

The red-belly toad, *Melanophryniscus stelzneri* (Weyenbergh, 1875) (Anura: Bufonidae), is a diurnal toad, endemic to the pampasic Sierras system of Córdoba and San Luis provinces in central Argentina, the southern distribution

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area of the genus. The species is commonly distributed in isolated populations throughout Sierras of Córdoba. They are small, black toads, with bright yellow spots on arm, shoulders and sides, and ventrally black with bright red spots on belly (Cei, 1980), displaying an aposematic design. Red-belly toads have seasonal reproduction, occurring from October until the end of the wet season in March; they are considered explosive breeders, highly synchronized with heavy rainfall (Cei, 1980; Gallardo, 1987). Therefore, multiple breeding events occur, depending on the rainfall frequency during the reproduction season. After a heavy rain, they congregate in large groups at breeding sites. Each amplectant pair deposits multiple egg masses per amplexus event. These clutches are laid in small groups (from 5 to 35 eggs) and fixed to submerged vegetation by the male while the pair is still in amplexus. Larval development is fast, spanning less than 30 days (Bustos Singer and Gutierrez, 1997).

Red-belly toads are exposed to several threats, such as dramatic habitat loss due to expansion in agricultural and tourism activities; harvest for international pet trade, without any control or monitoring of the number of individuals extracted. In addition, cases of anurans infected with chytridiomycosis were recorded in 2005 and 2006, confirming the presence of the fungus *Batrachochytrium dendrobatidis* in the locality of Villa Flor Serrana (Ghirardi et al., 2009), where this study was made. The finding of *Bd* in the study area represents a potentially serious threat to all amphibians of the region, because chytridiomycosis is one of the major causes of anuran extinctions and declines (Skerrat et al., 2007). All these threats can be synergistic; thus, in combination, these factors may result in reduced viability of anuran populations (Semlitsch, 2000). Therefore, further information about the species status and habitat choice is needed to develop strategies aimed at habitat protection and species conservation (Ficetola, Valota and de Bernardi, 2006).

Our objective was to investigate the relationship between reproductive activity of red-belly toads and features of water bodies used as breeding habitat in Córdoba province, Argentina, to understand the ecological factors that affect their occurrence. We hypothesized that reproductive activity of red-belly toads in a particular water body would depend on (1) pond morphology: small and shallow temporary ponds would not allow the establishment of potential large-sized predators such as fishes or competitors, such other anuran species; (2) biotic features: vegetation within and surrounding the pond and a muddy bank would provide food, shelter from predators and sites where to fix eggs; and (3) the presence of other organisms within the pond: to enhance their reproductive success, red-belly toads would use sites without the presence of potential predators or competitors.

Materials and methods

Study area

The study was conducted in the localities of Villa Flor Serrana and Mallín, Punilla department, Córdoba province, Argentina, at 800 m a.s.l. (S31°23′10.8″, W64°36′23.6″ and S31°19′18.0″, W64°35′04.6″, respectively). The physiognomy of the surrounding vegetation is that of sierra secondary forest and thorny shrubland, typical of the Chaco Serrano phytogeographic region (Cabrera, 1976). The landscape is gently undulating with occasional breakaway slopes and granite outcrops. The landscape is characterized by streams, flowing irregularly over granitic rock with a mean depth of 70-100 cm, and by small ephemeral ponds that dry up in the dry season (approximately April-September) and several times during the rainy period (October-March). A characteristic ephemeral wetland common throughout this region is the locally called *mallín*, which retains rain water temporarily. Due to its flooded and soft soil, the *mallín* presents small interconnected hollows that fill up with water. Most of the *mallines* occur in areas with mild slopes, which generate clear waters with a slight current. The effect of trampling by both livestock and other animals promotes the formation of hollows.

Annual rainfall is 900 mm, mainly concentrated from September to March. Mean annual temperatures ranged from 9.8°C to 21.5°C, with extreme values dropping below 0°C and occasionally exceeding 38°C.

Site surveys

Fieldwork was carried out from November 2007 to February 2008, in coincidence with the reproductive activity of the species (Bustos Singer and Gutierrez, 1993). We used diurnal visual and aural encounter surveys to evaluate the presence or absence of red-belly toads (Crump and Scott, 1994). We conducted weekly surveys between 8.00 and 13.00 hours, corresponding to the period of greatest anuran vocalization and activity. Each site was surveyed for at least 20 minutes. Breeding activity of red-belly toads was established by the detection of amplectant pairs, calling males, tadpoles and/or egg masses. Non-breeding sites were haphazardly selected on the basis of geographical proximity to the breeding sites used by the red-belly toads. As red-belly toad adults congregate in large groups at the breeding sites, have a loud advertisement call, and are bright-colored, they are highly detectable. Therefore, taking into account the characteristics of both adults and larvae of the species, the absence of red-belly toads was determined through weekly surveys. Both used and unused sites were surveyed on the same day. We considered a total of 30 sites where toads were breeding, and 30 nearby sites where toads were not breeding. All the ponds surveyed contained water at the onset of breeding season.

Habitat variables

We recorded eight variables that we considered important for the ecology of red-belly toads because they were previously shown to be important for other species of the genus (Bustos Singer and Gutierrez, 1993; Goldberg, Quinzio and Vaira, 2005), as well as for other anuran species (Vos and Chardon, 1998; Hazell et al., 2003; Johnson, Mahan and Semlitsch, 2008). Three parameters were related to morphological features of the pond: maximum width, depth, and hydroperiod. We measured maximum width with a tape measure, and depth of water body as average depth of water body determined by sounding with a weighted line. We also noted whether the water body was permanent or temporary. The category permanent water body included permanent ponds, rivers and streams. The temporary water body category comprised wetlands that dried up during the breeding season (temporary ponds, *mallines* and springs). Wetland types were not used in GLM analysis because they were nested within the categories permanent and temporary wetlands, but were useful in determining the precise type of wetland used by red-belly toads. Vegetation variables included: the percentage of vegetation cover surrounding the water body, the percentage of both submerged and emergent vegetation covering the water surface, and the substrate type to describe the biotic features of ponds. The substrate was classified into three types: mud, mud and stones, and stones. The presence of other organisms within the pond was assessed by recording the presence of heterospecifics breeding at focal sites (based on the presence of eggs or tadpoles) and potential predators of eggs and larvae (e.g., snails, odonate naiads, bellostomatids and fishes) using visual and net surveys.

Statistical analysis

We compared the frequency of used and unused sites of different water body types using a χ^2 test. We report descriptive statistics as median $\pm$ SD, unless otherwise noted. We performed Mann-Whitney U test for continuous variables and contingency tables for discrete variables to compare the different features between used and unused sites.

We used an information-theoretic approach (Burnham and Anderson, 2002; Mazerolle, 2006) to evaluate the relative support for the different hypotheses in explaining habitat selection by red-belly toads. First we formulated three a priori candidate models, each representing a biological hypothesis, to explain the presence of red-belly toads. The first model (morphological features model) included three independent variables: water body width and depth, and hydroperiod. The second model (biotic features model) included three independent variables: percentage of vegetation surrounding the water body, percentage of water surface covered by vegetation, and substrate type. The third model (other organisms' model) included two variables: presence or absence of potential predators, and presence or absence of other anuran species. We then built all possible combinations of these models, obtaining seven a priori models (table 2).

To ensure independence of predictor variables, we calculated Pearson correlation coefficients for all pairwise combinations of independent variables. We considered $r \geqslant 0.70$ a suitable criterion for omitting a variable (Fielding and Haworth, 1995; Tabachnick and Fidell, 1996). Because correlation coefficients ranged well below the suggested cutoff, all independent variables were therefore included in the analysis.

We used GLM assuming binomial error (i.e., logistic regression) to evaluate the relationship between the independent variables predicted to be important by the a priori models and the presence of breeding activity of red-belly toads (Denöel et al., 2009). We then calculated Akaike's Information Criterion (AIC) to assess the strength of evidence for each model. The model with the lowest AIC value is the one best supported by the data (Burnham and Anderson, 2002). The use of AIC corrected for small sample size (AICc) is controversial, and simulation studies suggest that AICc does not perform better than AIC (Richards, 2005; Manenti, Ficetola and de Bernardi, 2009); therefore, we report the results obtained using AIC. We calculated the Δ AIC. Models of less than 2 AIC units from the best model are usually considered good candidates. Values between 3 and 7 indicate that the model has considerably less support, whereas a delta AIC bigger than 10 indicates that the model is very unlikely (Burnham and Anderson, 2002). We calculated AIC weights w_i for each model, which represents the probability that a model is the best in the whole set of candidate models, and the cumulative AIC weight w for each variable, which stands for the relative importance of each variable. We also calculated the evidence ratios $E = w_i/w_j$ to compare the relative strength of evidence for two hypotheses (Lukacs et al., 2007) and Nagelkerke's R^2 (R^2_N), as a measure of predictive efficiency of the models. Probability was considered significant at of 0.05 or less. Lastly, we evaluated the strength of the best model by verifying that zero was not encompassed by the model-averaged regression coefficient and its unconditional standard error for each of the environmental variables included in the models (Burnham and Anderson, 2002; Mazerolle, 2006).

Results

Reproduction of red-belly toads was recorded in all water body types considered, with the exception of rivers. In this study, breeding red-belly toads presented a significant association with *mallines*. Although *mallines* are not the most abundant sites in the study area, all of them were used as breeding sites. Springs also showed a significant association, but due to the low number of sites sampled we did not considered this category for further discussion (fig. 1). All water bodies identified as breeding sites were used repeatedly by the red-belly toads during the reproductive season, indicating that egg laying in these sites was not occasional.

Water bodies used by red-belly toads as spawning sites differed from unused nearby sites in several aspects. Most toads spawned in small, muddy-banked shallow pools, with comparatively greater vegetation covering the water surface and around the ponds than in unused ponds. Red-belly toads generally used ephemeral ponds where there were no potential predators or other anuran species (table 1).

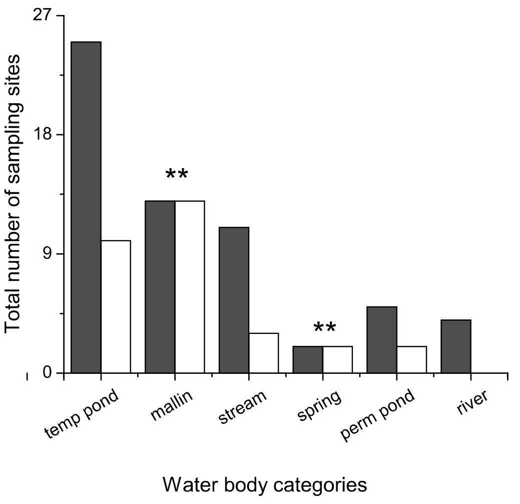

Figure 1. Bar chart showing the frequency distribution of different water body types for the total number of sampled sites (grey bars) and the number of water bodies occupied by the red-belly toads (white bars). The asterisks show a significant difference in use between the different sites sampled (test χ^2 $p < 0.05$).

Our best model suggested that morphology, biotic features and the presence of other organisms are important to explain the presence of breeding activity of the red-belly toads (table 2). According to AIC weights, the probability that this was the best model, based on the data, was 0.783. The second best model suggested that only biotic features and the presence of other organisms within the pond were important to explain the presence of breeding activity of red-belly toads (AIC weight $= 0.149$). Based on the AIC evidence ratios, this model was five times less likely to be the best model. The best model explained 71% of variance in the data (Nagelkerke's R^2) and strongly suggested that red-belly toad females do not lay eggs randomly. All the other alternative models had much lower support than the best model presented.

Both the proportion of vegetation covering the water surface and surrounding the pond was positively correlated with breeding site use, which shows that the red-belly toad prefers spawning sites with abundant vegetation inside the water body. Red-belly toad presence was negatively associated with pond depth but positively associated with pond width. They also showed a preference for ephemeral muddy sites and a negative association with ponds with presence of other anuran species or potential predators (table 2). All variables were strongly associated with the presence of reproductive activity of red-belly toads since the model-averaged regression coefficient did not overlap zero. The biological variables presented higher cumulative AIC weight values than the structural features of the water body (table 3).

Discussion

Our results showed that red-belly toads (*Melanophryniscus stelzneri*) exhibited non-

Table 1. Median values ± SD of eight microhabitat variables and percentage of categorical variables in sites with or without red-belly toads (*Melanophryniscus stelzneri*). WType: Water body type; VegPer: Percentage of vegetation cover surrounding the water body; VegWat: Percentage of vegetation covering the water body surface.

Variable	Toads present		Toads absent		p
	Median	SD	Median	SD	
Width (m)	1.43	±1.55	2.02	±1.05	0.0046
Depth (cm)	10.33	±8.62	19	±12.11	0.0016
VegPer (%)	0.9	±0.16	0.67	±0.25	0.0001
VegWat (%)	0.67	±0.29	0.32	±0.27	<0.0001
WType					0.0023
Permanent	21		79		
Temporary	63		37		
Substrate					0.0008
Mudd	80		30		
Mudd and stone	20		57		
Stone	0		13		
Predators	33		80		0.0003
Anurans	43		63		0.0007

Table 2. A priori habitat models, and their rank, based on AIC values. k: number of parameters for each model; ΔAIC: Differences between AIC of a model and the best AIC; w_i: Akaike's weight of the model; R^2_N: Nagelkerke's R^2. WType: water body type (temporary or permanent); VegPer: percentage of vegetation cover surrounding the water body; VegWat: percentage of vegetation covering the water body surface; Subs: substrate dominant composition; Pred: presence or absence of potential predators.

Rank	Variables	k	ΔAIC	w_i	R^2_N
1	Depth Width WType VegPer VegWat Subs Pred Anura	8	0	0.7837	0.72
2	VegPer VegWat Subs Pred Anura	5	3.32	0.1492	0.62
3	Depth Width Wtype VegPer VegWat Subs	6	5.33	0.0547	0.60
4	VegPer VegWat Subs	3	8.60	0.0106	0.50
5	Depth Width WType Pred Anura	5	12.73	0.0014	0.47
6	Pred Anura	2	15.37	0.0004	0.34
7	Depth Width Wtype	3	19.50	<0.0001	0.30

Table 3. Model-averaged parameters of pond features explaining the presence of reproductive activity of red-belly toads. w: cumulative AIC weight of each variable; b: average regression coefficient, with their Unconditional SE. WType: water body type; VegPer: percentage of vegetation cover surrounding the water body; VegWat: percentage of vegetation covering the water body surface. The categories of discrete variables are shown in parenthesis.

Variables	w	b	SE
WType (temporary)	0.840	2.370	1.200
Substrate (mud)	0.998	22.241	16.915
Substrate (mud and stone)	0.998	21.798	16.064
Width	0.840	−0.455	0.337
Depth	0.840	0.042	0.026
Predators (absence)	0.935	1.192	0.657
Anura (absence)	0.935	2.277	1.195
VegPer	0.998	3.564	2.774
VegWat	0.998	3.023	2.210

random habitat use at the spatial scale examined, with a clear preference for ephemeral and shallow breeding sites, with abundant vegetation both within and surrounding the water body, and with absence of potential predators and other anuran species.

Habitat-suitability models are based on the assumption that the selected key factors are habitat parameters of major ecological importance, e.g., those that might affect development, growth and/or survival of the larvae in some way (Rudolf and Rödel, 2005).

The biological features were most important in explaining the presence of reproductive activity of red-belly toads. Preference for ponds with abundant vegetation may merely represent a by-product of life-history needs by red-belly toads, due to their behaviour of fixing the eggs to submerged plants near shallow coasts (Lavilla and Rouges, 1992; Bustos Singer and Gutierrez, 1997). On the other hand, the amount of vegetation cover within the ponds may generate complex microhabitats within the water body that could provide shelter from potential predators (Egan and Paton, 2004) and food for larvae. Vegetated ponds may be favourable sites for red-belly toads, since tadpoles tend to be poor swimmers and stay at the bottom of water bodies, hidden among stones or vegetation (Bustos Singer and Gutierrez, 1997). This can be a critical factor for the survival and development of larvae in this environment. In addition, the high amount of vegetation within and surrounding the selected ponds might generate a more stable thermocline, not only during the day by avoiding a quick rise of water temperature, but also during the breeding season, reducing the risk of desiccation. Hence, given the species' preference for ephemeral ponds, a high percentage of vegetation cover both within and around the pond seems extremely important.

The common use of sites disturbed by livestock trampling, as *mallines*, has also been observed in a congeneric species. Goldberg, Quinzio and Vaira (2006) suggested that the presence of this disturbance allows the formation of small water bodies which may be optimal reproductive sites for *Melanophryniscus rubriventris* and other species requiring a similar habitat. Furthermore, Goldberg, Quinzio and Vaira (2006) also observed that the species avoided riverine systems for oviposition, which is consistent with the present results.

As reported by Bustos Singer and Gutierrez (2003), larvae of red-belly toads have a fast metamorphosis period of less than 30 days. One of the advantages of the ephemeral nature of this breeding behaviour, besides small pond size, is that it may help to limit the presence of certain organisms and avoid the establishment of others, such as large-sized aquatic macroinvertebrates, fishes or other anuran species which may become predators or resource competitors (Heyer, McDiarmind and Weigmann, 1975; Heyer, 1976; Babbitt and Tanner, 1998; Snodgrass et al., 2000; Baber et al., 2004). Pond morphology is as important as the presence of other organisms in the pond. The composition of temporary pond community largely affects larval performance of most species (Resertarits and Wilbur, 1989). The absence of potential predators and competitors can increase the probability of reproductive success of red-belly toads (Resetarits and Wilbur, 1989; Rieger, Binckley and Resetarits, 2004).

The synchronization of the rainy season and reproductive activity of red-belly toads in ephemeral ponds (Gallardo, 1974; Cei, 1980) seems to be an adaptive response to fluctuations in environmental conditions, reducing the risk of reproductive failure due to desiccation (Goldberg, Quinzio and Vaira, 2006). The reproductive characteristics of this species, explosive breeding synchronized with rainfalls and fast larval development, seem salient for congeneric (Fernández, 1927; Prigioni and Garrido, 1989; Bustos Singer and Gutierrez, 1997; Vaira, 2005; Goldberg, Quinzio and Vaira, 2006) and numerous anuran communities from areas with a markedly seasonal climate in South America (Prado, Uetanabaro and Haddad, 2005).

The results of this study suggest that red-belly toad adults somehow perceive variation in the quality of aquatic mountain environments, and therefore they use differentially some water bodies of particular physical and biological characteristics, such as *mallines.* In light of the potential threats the species may be exposed to and taking into account its restricted distributional range, it is important that we understand basic data of the species to monitor populations trends and develop appropriate conservation strategies. Further studies, such as those concerning larval survival rates and body condition of metamorphic individuals, are needed to assess the differential fitness of red-belly toads in different breeding habitats.

On the other hand, although ephemeral ponds, like *mallines*, are highly vulnerable to human activities and threatened in many regions, their biodiversity value is frequently overlooked, contributing to their neglected and inadequate management (Beja and Alcazar, 2003). For certain species, these types of wetlands are critical habitats, and species strongly associated with these water bodies may not persist in landscapes in which the loss of these wetlands is significant (Babbitt, 2005).

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