Journal of Natural History
Vol. 45, Nos. 29–30, August 2011, 1789–1799

Taylor & Francis
Taylor & Francis Group

Vocal repertoire of two species of *Oreobates* Jiménez de la Espada, 1872 (Anura: Strabomantidae) of the Yungas Andean Forest, NW Argentina

Mauricio S. Akmentins*

CONICET-Centro de Investigaciones Básicas y Aplicadas(CIBA), Universidad Nacional de Jujuy, Gorriti 237 (4600), San Salvador de Jujuy, Argentina-Instituto de Bio y Geociencias del NOA (IBIGEO), Museo de Ciencias Naturales, Universidad Nacional de Salta, Mendoza 2 (4400), Salta, Argentina

(Received 7 July 2010; final version received 3 February 2011; printed 2 June 2011)

The vocal repertoire of males of two cryptic species of *Oreobates* and interpretation of the communicative significance of vocalizations were studied under natural conditions in Yungas Andean Forest of NW Argentina. Males of *O. discoidalis* and *O. barituensis* showed remarkable territorial behaviour defending their calling sites against conspecific males through both aggressive vocalizations and fights involving physical contact. The vocal repertoire of both species consists of at least three different call types. Two of these vocalizations, advertisement calls and territorial calls were utilized in long-range territorial interactions, and aggressive calls were utilized in close-range male-male territorial interactions. This represents the first report of a complex repertoire of vocalizations in the genus *Oreobates*

Keywords: aggressive vocalizations; encounter calls; territorial calls; Terrarana

Introduction

Based primarily on molecular evidence, the New World direct-developing frogs were recently placed into a new taxon, Terrarana (Hedges et al. 2008). Remarkable for not only their specialized terrestrial reproductive mode, this enormous taxon (with nearly 900 described species) garners excessive interest because members display an unusual array of reproductive adaptations including parental care by males or females, internal fertilization and ovoviviparity (Townsend and Stewart 1986). In addition, taxon members also exhibit a diversity of vocal repertoires used in complex social behaviours and interactions (Wells 1981; Woolbright 1985; Wilczynski and Brenowitz 1988; Ovaska and Hunte 1992; Ovaska and Caldbeck 1997a; Ovaska and Rand 2001).

In many geographic areas, terraranans have evolved sympatrically in dense species assemblages where selective pressures for reproductive isolation and acoustic interference avoidance, among others, may have contributed to the remarkable array of vocalizations (Drewry and Rand 1983). The few species whose vocal behaviour has been studied in detail show great diversity in vocalizations and call variation associated with different behaviours, including advertisement (Drewry and Rand 1983), courtship (Michael 1996; Ovaska and Caldbeck 1997b, 1999), aggression (Wilczynski and Brenowitz 1988; Stewart and Rand 1992), female reciprocal call (Schlaepfer and Figueroa-Sandí 1998; Díaz and Estrada 2000), retreat site defence (Stewart and Rand 1991; Michael 1997), and nest site defence (Stewart and Rand 1991).

*Email: msakmentins@conicet.gov.ar

ISSN 0022-2933 print/ISSN 1464-5262 online

DOI: 10.1080/00222933.2011.560967
http://www.informaworld.com

The presence of an advertisement call that may function both in mate attraction and inter-male spacing is an almost ubiquitous feature in anuran communication systems, but males of most species also produce a variety of specific calls that are used when encountering females or other males (Wells 1977). Aggressive calls are an important component of the vocal repertoire of many anurans (Wells 1977), and by shifting from advertisement to aggressive calls, a male can signal his awareness and intention to defend his territory through physical aggression to potential intruders (Wells 1988). A continuous and increasing level of aggressive vocalizations may be emitted by territorial males, from long-range "territorial calls" to short-range "encounter calls", and these aggressive behaviours are elicited by thresholds mediated by acoustic and/or visual cues (Wells 2007). Examination of the structure and function of these calls provides a potentially fruitful field for investigating the constraints and driving forces that have shaped vocal communication within this vast group of frogs (Ovaska and Caldbeck 1997a).

In recent years, bioacoustical investigations of advertisement calls have led to the description of several new species of the genus *Oreobates* Jiménez de la Espada, 1872 (Padial et al. 2008; Vaira and Ferrari 2008), the genus with the southernmost distribution of the highly diverse family Strabomantidae (Hedges et al. 2008). Most of the species in the genus *Oreobates* are still poorly understood, primarily because of their remote nature (inhabiting thick understory of steepest Andean tropical forests) and difficulty of detecting them in the field due to low densities and erratic calling behaviour, making recording a nearly impossible task (Padial et al. 2008).

The subtropical humid montane forests of NW Argentina are inhabited by two sympatric species of Strabomantidae, *Oreobates discoidalis* (Peracca, 1895) and the recently described *Oreobates barituensis* Vaira and Ferrari, 2008 (Lavilla et al. 2000; Akmentins and Vaira 2009). These small frog species are almost morphologically indistinguishable and are mainly identified in the field by advertisement calls (Ferrari and Vaira 2008; Vaira and Ferrari 2008). Despite recent attention however, several aspects of the biology, ecology and behaviour of these frogs remain unknown.

The main objective of this work was to provide a descriptive analysis of vocal repertoire and interpretation of the social context to the vocalizations of terraranan frogs *O. discoidalis* and *O. barituensis* of Yungas Andean Forest in NW Argentina.

Materials and methods

From September to January between 2007 and 2010, coincident with the breeding period of the species (Vaira 2002), I conducted weekly surveys of male calling behaviour of *O. discoidalis* and *O. barituensis* in six localities in the range of both species in the Yungas montane forest of Jujuy and Salta provinces in NW Argentina (Table 1). Behavioural observations of calling males were conducted between 20:00 and 02:00 h, corresponding to the period of greatest vocalization activity for the two species. I used nocturnal visual and aural encounter surveys to localize the active calling males (Heyer et al. 1994). Territorial interactions between calling males were registered *ad libitum* (Altmann 1974) and vocalizations were recorded when possible, using an Olympus Vn-6200 digital recorder. The length of recording depended of the duration of vocal interaction between males.

Table 1. Localities visited during fieldwork.

Locality	Geographic coordinates	Altitude (m)
Jaire	24° 01′ S; 65° 23′ W	1703
Abra de Cañas	23° 40′ S; 64° 53′ W	1722
Abra Honda	23° 40′ S; 64° 55′ W	1574
Río Yerba Buena	23° 30′ S; 64° 56′ W	1457
Arroyo La Loza	23° 28′ S; 64° 56′ W	1622
El Arazay	22° 18′ S; 64° 42′ W	1614

For each territorial interaction the vocalization site of calling males was noted and classified in a general category (bare ground, leaf litter, rock and fallen trunks). In conjunction with this, the distance to the closest calling male was also measured. Air temperature at the ground level was measured with a digital thermometer to the nearest 0.1°C. For each male, territorial interaction was registered once per night, because males were removed from the vocalization sites for trophic ecology studies.

Calls were digitized and analysed to obtain numerical information and to generate audiospectrograms and oscillograms using Soundruler software (Gridi-Papp 2004). Sampling frequency was 44.100 Hz at 16-bit resolution. Frequency information was obtained through fast Fourier transformation (width 256 points) at hamming window function. For each specimen recorded, five complete vocalizations were analysed. Quantitative parameters were expressed as mean ± standard deviation. The terminology used for the description of calls follows Heyer et al. (1990); "note" was used as the functional unit of a call, and "pulse" as subunits that form a note (Giasson and Haddad 2006). Aggressive call characteristics were compared with published advertisement call descriptions of *O. discoidalis* (Ferrari and Vaira 2008) and *O. barituensis* (Vaira and Ferrari 2008).

Results

Males of *O. discoidalis* and *O. barituensis* showed remarkable territorial behaviour, defending their calling sites against conspecific males through both aggressive vocalizations and fights involving physical contact. Aggressive calls included long-range territorial calls and short-range encounter calls (Table 2).

O. discoidalis aggressive vocalizations

Male territorial calls were frequently heard at dusk during the beginning of calling activities or in full choruses interspersed with advertisement calls when two males called in close proximity to one another (Figure 1). All registered males called under dense understory at ground level (39 males), they called from rocks (18 males), leaf litter (14 males), or fallen trunks (seven males).

The territorial call consisted of two or three short repeated notes (119.16 ms), with a mean dominant frequency of 2012.9 Hz and was sometimes accompanied by a second and third harmonic at 4100 Hz and 6200 Hz (Figure 1).

Table 2. Temporal and numerical parameters of the vocal repertoires of *Oreobates discoidalis* and *Oreobates barituensis* from NW Argentina. The means of parameters ± SD are followed by ranges in the parentheses.

	Advertisement call *O. discoidalis*	Territorial call *O. discoidalis*	Encounter call *O. discoidalis*	Advertisement call *O. barituensis*	Territorial call *O. barituensis*	Encounter call *O. barituensis*
Calls analysed (specimens)	10 (2)	30 (6)	30 (6)	10 (2)	10 (2)	10 (2)
Air temperature (°C)	20.2	13.6–22.1	17.4–20.3	17.5	18.2–21.2	18.2–21.2
Call length (ms)	634 ± 57.13 (550–720)	119.16 ± 44.06 (77.4–182)	136.56 ± 12.47 (122.2–151.2)	185.3 ± 18.9 (168–211)	9.8 ± 0.28 (9.6–10)	128.12 ± 5.83 (124–132.25)
Notes per call	11.6 ± 1.14 (10–13)	2.36 ± 0.44 (2–3)	1	5.3 ± 0.5 (5–6)	1	2
Note rate (note s^{-1})	18.2 ± 0.27 (18–18.7)	21.13 ± 3.57 (16.54–25.9)	—	30.6 ± 1.01 (29.5–32)	—	15.69 ± 0.62
Note duration (ms)	31.69 ± 3.33 (24–40)	13.75 ± 1.17 (11.7–14,86)	—	4.3 ± 1.0 (2–6)	—	97.12 (1° note) 17.37 (2° note)
Frequency band (Hz)	1702–2552	1798.74–2295.9	1601.46–2075.4	—	1688.6–2058.9	1457.62–1855.25
Dominant frequency (Hz)	2068 ± 63.5 (1902–2164)	2012.9 ± 79.18 (1872.18–2083.3)	1759.18 ± 62.1 (1661.16–1845.84)	3226 ± 121.26 (2916–3449)	1791.37 ± 75.27 (1738.14–1844.6)	1580.35 ± 94.57 (1513.47–1647.22)
Inter-note (ms)	23.44 ± 2.97 (13–31)	59.73 ± 7.78 (47.4–68.77)	—	—	—	13.15 ± 3.32 (10.8–15.5)
Source	Ferrari and Vaira (2008)	Current work	Current work	Vaira and Ferrari (2008)	Current work	Current work

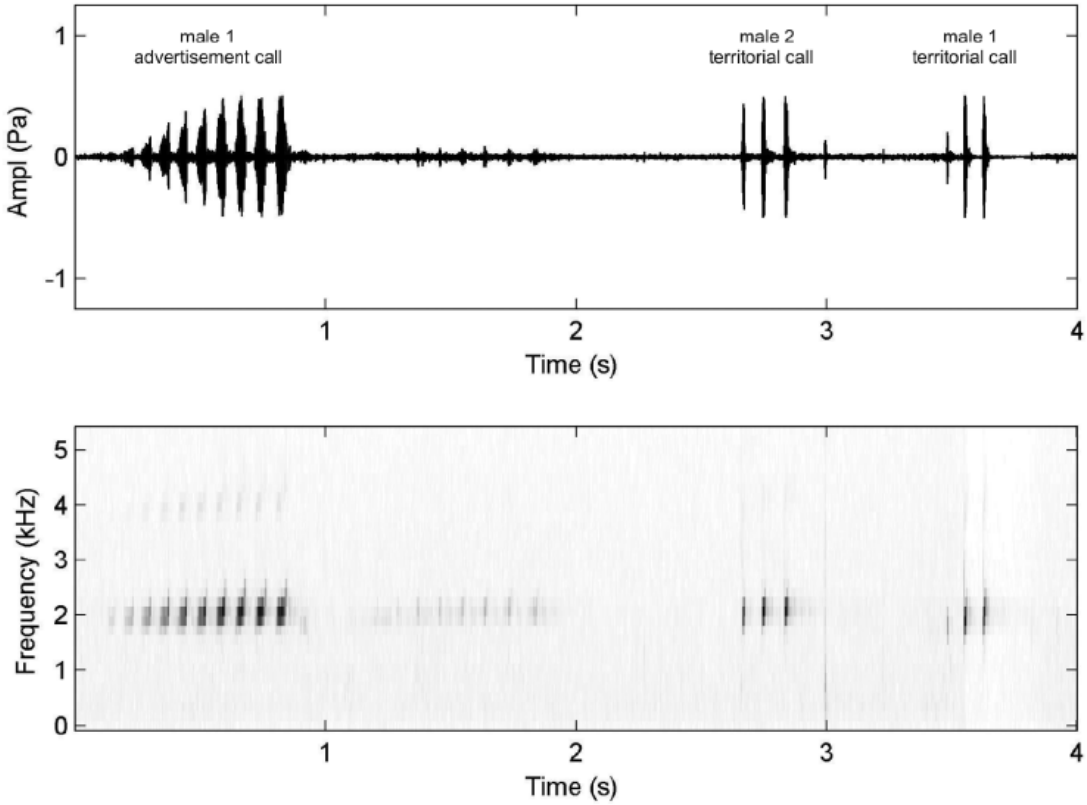

Figure 1. Oscillogram and sound spectrogram of the advertisement call and territorial call of *Oreobates discoidalis* from Jaire, Jujuy province, Argentina. Recorded on 8 November 2009; air temperature during recording was 13.6°C.

Nearest neighbour mean distance between calling males was 4.06 m (18 pairs of males). Measuring the nearest neighbour distance for this species was difficult, because often the males nearest to the sampled calling male were disturbed and stopped their calling activities.

Encounter calls were registered on several occasions. Squeals emitted during fights were produced by one or both males involved in the struggle; this call was produced both during physical altercations (two events), and by males separated by distances < 30 cm (three events). This aggressive behaviour was only observed for close-range interactions between males. This was a one note call (mean call length: 136.56 ms), with a mean dominant frequency of 1759.18 Hz and with a second harmonic at 3500 Hz (Figure 2).

Territorial and encounter calls were shorter and with fewer notes than advertisement calls (634 ms; 10–13 notes per call). Territorial call notes had similar dominant frequency to the advertisement call, but encounter calls had a lower dominant frequency than the other two types of calls. Similar to the advertisement call, aggressive call harmonics were present but they were diffuse and not obvious in most calls (Figure 2).

O. barituensis aggressive vocalizations

Territorial calls were produced in circumstances quite similar to those of *O. discoidalis*. All registered males called from bare ground in small cliffs of clay rock without vegetative covering (14 males). Distances between calling males were smaller than

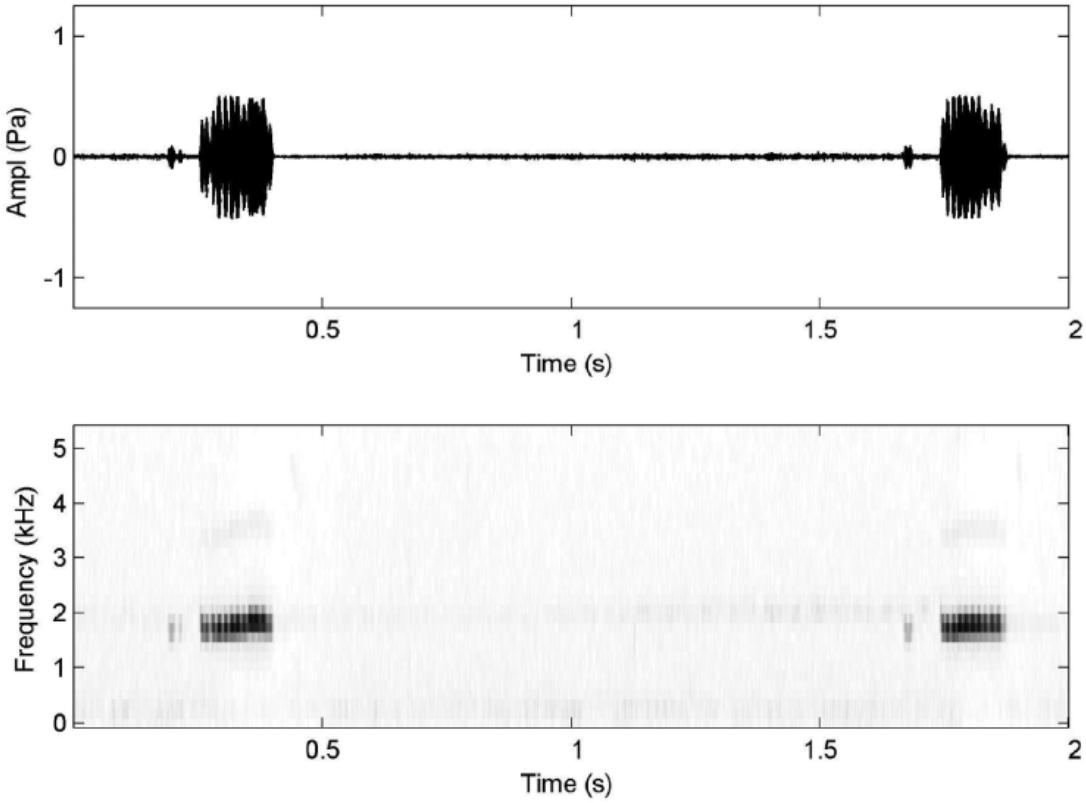

Figure 2. Oscillogram and sound spectrogram of the encounter call of *Oreobates discoidalis* from Jaire, Jujuy province, Argentina. Recorded on 14 November 2009; air temperature during recording was 17.4°C.

those registered for *O. discoidalis*; nearest neighbour mean distance for calling males was 1.82 m (seven pairs of males). Territorial calls consisted of one short note (mean call length of 9.8 ms) with a mean dominant frequency of 1791.37 Hz and no harmonic structure present (Figure 3).

Encounter calls were registered both during physical encounters (bumping struggle, one event) and between males separated by a distance < 30 cm (two events). As in *O. discoidalis*, this behaviour was only observed for close-range interactions between males. This squeal had two different duration notes, the first note with a mean note length of 97.12 ms (range 97 to 97.25 ms) and a shorter second note with a mean note length of 17.37 ms (range 17 to 17.75 ms). Both aggressive notes had similar dominant frequencies with a mean of 1759.18 Hz and no harmonic structure present (Figure 4).

Aggressive calls of *O. barituensis* were shorter and with lower dominant frequencies than advertisement calls of this species (Table 2).

Discussion

Males of both *O. discoidalis* and *O. barituensis* had a vocal repertoire that consisted of at least three different call types used in territorial interactions between conspecific individuals. Two of these vocalizations, advertisement and territorial calls, were

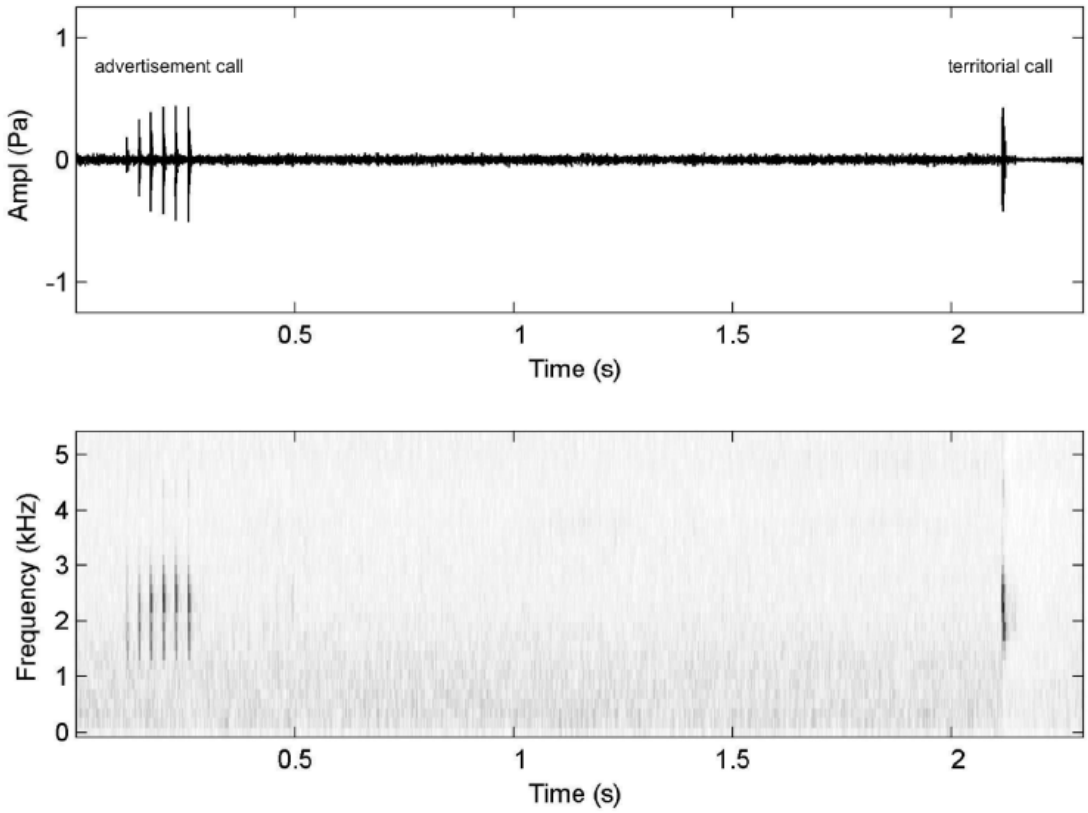

Figure 3. Oscillogram and sound spectrogram of the advertisement call and territorial call of *Oreobates barituensis* from Río Yerba Buena, Jujuy province, Argentina. Recorded on 1 December 2009; air temperature during recording was 21.1°C.

observed during long-range territorial interactions, while encounter calls were used in close-range territorial interactions.

Segregated specific microhabitats were used and defended actively for calling activities by males of both species, even if males cohabited in the same localities. Males of *O. discoidalis* used diverse sites for calling but always at ground level and under a dense understory environment, whereas males of *O. barituensis* called from bare ground in open areas disturbed by human activity (Vaira and Ferrari 2008; Akmentins and Vaira 2009). There are no available data about reproductive behaviour of these frogs (e.g. courtship, nesting site selection, parental care); this information could be useful in understanding possible calling site segregation and the nature of the defended resource, whether males defend a calling site (Wells 1981), and/or they defend an oviposition territory (Townsend 1989). Other possible explanations for calling microhabitat segregation are complementary prezygotic isolation mechanisms (Hödl 1977), or physiological differences between these two species reflected in calling site selection (Pough et al. 1977).

The structure of aggressive vocalizations of Argentinean *Oreobates* species differ markedly from the structure of advertisement calls in temporal and spectral features. The difference between aggressive and advertisement calls seems to be an ubiquitous trait in most terraranan males, although no general tendency in variation seems to exist within this taxon (Wells 1981; Stewart and Rand 1991; Michael 1997; Höbel

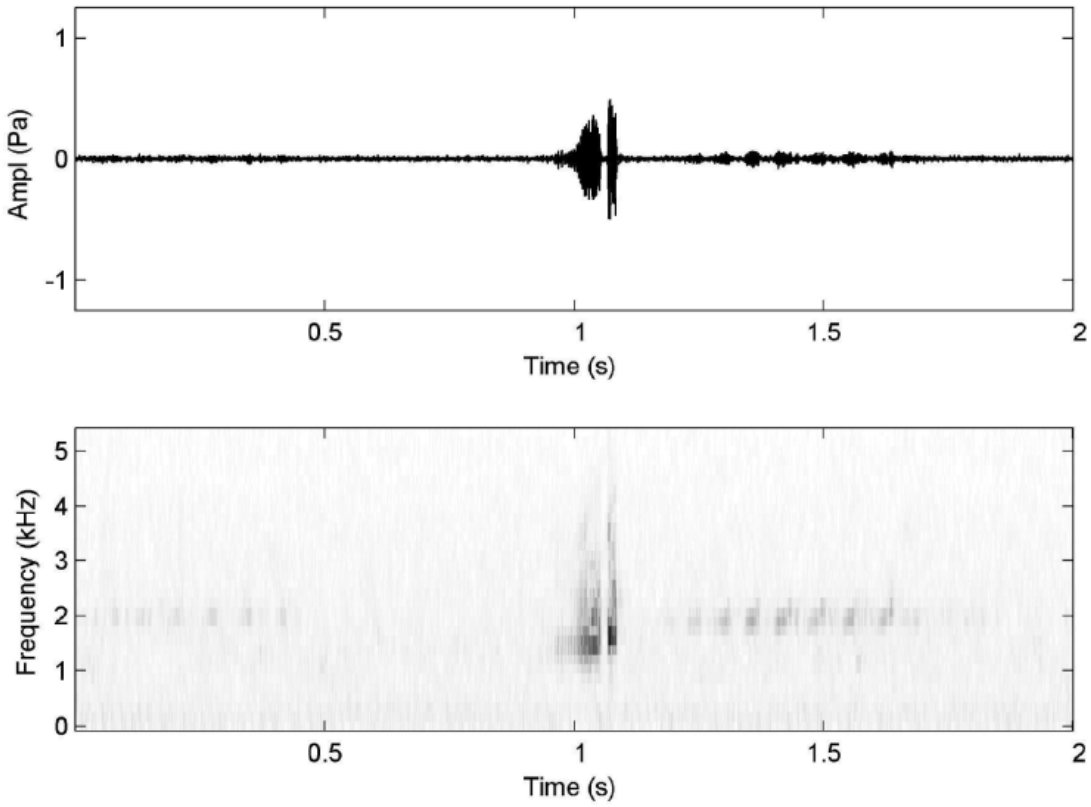

Figure 4. Oscillogram and sound spectrogram of the encounter call of *Oreobates barituensis* from Arroyo La Loza, Jujuy province, Argentina. Recorded on 29 November 2008; air temperature during recording was 18.0°C.

2005). The low intensity of the encounter call broadcast energy compared to that of the advertisement call of both species could be attributed to the close-range nature of these vocalizations. The low intensity of close range calls (courtship, mating, initiation of amplexus) reported in other terraranans may have occurred to avoid acoustic interference (Michael 1996; Ovaska and Caldbeck 1999). Alternatively, lowering of the decibel level during the close-range calls may conserve energy, or restrict the number of conspecifics and/or predators that would be aware of the frogs' presence (Felton et al. 2006).

Beyond structural differences in the spectral and temporal characteristics of aggressive vocalizations of the males of *O. discoidalis* and *O. barituensis*, both species shared similar social contexts of interactions between conspecifics and vocal repertoire structure. Males switched from trilled advertisement calls to short "click" aggressive vocalizations in long-range territorial interactions and produced "squeals" during close-range encounters. These similarities in social organization and vocal repertoire could be due to the phylogenetic proximity of these species (Vaira and Ferrari 2008).

Aggressive vocalizations are an important component in the social structure of diverse lineages of neotropical anurans with prolonged breeding seasons, such as Hylidae (Toledo and Haddad 2005), Centrolenidae (Greer and Wells 1980), Hemiphractidae (Sinsch and Joermann 1989), Hylodidae (Haddad and Giaretta 1999), Aromobatidae (Juncá 1998), Dendrobatidae (Forti et al. 2010) and

Leptodactylidae (Menin et al. 2009); among the families of Terrarana, territorial calls were registered in Eleutherodactylidae (Stewart and Rand 1992), Strabomantidae (Wells 1981) and Craugastoridae (Höbel 2005). This kind of aggressive vocalization may signal the motivational state of the opponents during agonistic encounters, helping to avoid the risks of physical combats (Haddad and Giaretta 1999). Like most direct-developing terraranans, calling males of *Oreobates* are widely distributed on the forest floor during the reproductive season because they are not limited to water bodies for reproduction. As such, aggressive vocalizations could play a fundamental role in the inter-male spacing and maintenance of calling territories or nesting sites throughout the reproductive season (Wilczynski and Brenowitz 1988). More precise information about the reproductive biology of these species is needed to elucidate the structure of mating systems and the function of vocal repertoire in such a system. In a "lek" system, males defend sites as territories and females control oviposition sites, meanwhile in a "resource defence" system males defend an oviposition site inside their calling territories (Wells 2007).

The presence of two types of aggressive vocalizations suggests that males may be able to respond in a graded fashion to increasing levels of intrusion/competition. Studies are needed to understand the social structure and interactions between conspecific individuals of Argentinean species of *Oreobates*, and playback experiments with vocal repertoires could help to elucidate which signals and thresholds elicit this graded aggressive communication system.

Acknowledgements

I thank K. A. Stewart and M. Vaira for helpful suggestions on the manuscript; L. C. Pereyra for valuable collaboration during field works and manuscript preparation; Administración de Parques Nacionales (APN) for permission to study anurans at PN Calilegua, PN Baritú and RN Nogalar de Los Toldos (DISPOSICION N° 49/08 and N° 24/09); CONICET and Carrera del Doctorado en Ciencias Biológicas de la FCEFN de la UNC; also anonymous reviewers for comments that greatly improved the manuscript.

References

Akmentins MS, Vaira M. 2009. Amphibia, Anura, Strabomantidae, *Oreobates barituensis*: Distribution extension, new provincial record and geographic distribution map. Check List. 5(2):216–217.

Altmann J. 1974. Observational study of behavior: sampling methods. Behavior. 49(3/4):227–267.

Díaz LM, Estrada AR. 2000. The male and female vocalizations of the Cuban frog *Eleutherodactylus guanahacabibes* (Anura: Leptodactylidae). Carib J Sci. 36(3/4):328–331.

Drewry GE, Rand AS. 1983. Characteristics of an acoustic community: Puerto Rican frogs of the genus *Eleutherodactylus*. Copeia. 1983(4):941–953.

Felton A, Alford RA, Felton AM, Schwarzkopf L. 2006. Multiple mate choice criteria and the importance of age for male mating success in the microhylid frog, *Cophixalus ornatus*. Behav Ecol Sociobiol. 59:786–795.

Ferrari L, Vaira M. 2008. Descripción del canto de anuncio de una población Argentina de *Oreobates discoidalis* (Anura: Strabomantidae). Cuad Herp. 22(2):82–85.

Forti LR, Strüssmann C, Mott T. 2010. Acoustic communication and vocalization microhabitat in *Ameerega braccata* (Steindachner, 1864) (Anura, Dendrobatidae) from midwestern Brazil. Braz J Biol. 70(1):211–216.

Giasson LOM, Haddad CFB. 2006. Social interactions in *Hypsiboas albomarginatus* (Anura: Hylidae) and the significance of acoustic and visual signals. J Herpetol. 40(2):171–180.

Greer BJ, Wells KD. 1980. Territorial and reproductive behavior of the tropical American frog *Centrolenella fleischmanni*. Herpetologica. 36(4):318–326.

Gridi-Papp M. 2004. Soundruler. Version 0.9.4.1. [Internet]. [cited 2010 July 01]. Available from http://soundruler.sourceforge.net.

Haddad CFB, Giaretta AA. 1999. Visual and acoustic communication in the Brazilian torrent frog, *Hylodes asper* (Anura: Leptodactylidae). Herpetologica. 55(3):324–333.

Hedges SB, Duellman WE, Heinicke MP. 2008. New World direct-developing frogs (Anura: Terrarana): Molecular phylogeny, classification, biogeography, and conservation. Zootaxa. 1737:1–182.

Heyer WR, Rand AS, Gonçalvez da Cruz CA, Peixoto OL, Craig EN. 1990. Frogs of Boracéia. Arq Zool. 31(4):231–410.

Heyer WR, Donnelly MA, McDiarmid RW, Hayek LC, Foster MS, editors. 1994. Measuring and monitoring biological diversity. Standard methods for amphibians. Washington, DC: Smithsonian Institution Press.

Höbel G. 2005. On the acoustic communication system of *Eleutherodactylus fitzingeri* (Anura: Leptodactylidae). Herp Rev. 36(3):242–244.

Hödl W. 1977. Call differences and calling site segregation in anuran species from central Amazonian floating meadows. Oecologia. 28:351–363.

Juncá FA. 1998. Reproductive biology of *Colostethus stepheni* and *Colostethus marchesianus* (Dendrobatidae), with the description of a new anuran mating behavior. Herpetologica. 54(3):377–387.

Lavilla EO, Vaira M, Ponssa ML, Ferrari L. 2000. Batracofauna de las Yungas Andinas de Argentina: Una síntesis. Cuad Herp. 14(1):5–26.

Menin M, Almeida APd, Kokubum MNdC. 2009. Reproductive aspects of *Leptodactytus hylaedactylus* (Anura: Leptodactylidae), a member of the Leptodactylus marmoratus species group, with a description of tadpoles and calls. J Nat Hist. 43(35–36):2257–2270.

Michael SF. 1996. Courtship calls of three species of *Eleutherodactylus* from Puerto Rico (Anura: Leptodactylidae). Herpetologica. 52(1):116–120.

Michael SF. 1997. Vocalization and diurnal retreat defense in the Puerto Rican frog *Eleutherodactylus cochranae*. J Herpetol. 31(3):453–456.

Ovaska K, Caldbeck J. 1997a. Vocal behaviour of the frog *Eleutherodactylus antillensis* on the British Virgin Islands. Anim Behav. 54:181–188.

Ovaska K, Caldbeck J. 1997b. Courtship behavior and vocalizations of the frogs *Eleutherodactylus antillensis* and *E. cochranae* on British Virgin Islands. J Herpetol. 31(1):149–155.

Ovaska K, Caldbeck J. 1999. Courtship call of the frog *Eleutherodactylus schwartzi* from the British Virgin Islands. J Herpetol 33(3):501–504.

Ovaska K, Hunte W. 1992. Male mating behavior of the frog *Eleutherodactylus johnstonei* (Leptodactylidae) in Barbados, West Indies. Herpetologica. 48(1):40–49.

Ovaska K, Rand AS. 2001. Courtship and reproductive behavior of the frog *Eleutherodactylus diastema* (Anura:Leptocatylidae) in Gamboa, Panama. J Herpetol. 35(1):44–50.

Padial JM, Köhler J, Muñoz A, de la Riva I. 2008. Assessing the taxonomic status of tropical frogs through bioacoustics: geographical variation in the advertisement calls in the *Eleutherodactylus discoidalis* species group (Anura). Zool J Linn Soc. 152(2):353–365.

Pough FH, Stewart MM, Thomas RG. 1977. Physiological basis of habitat partitioning in Jamaican *Eleutherodactylus*. Oecologia. 27:285–293.

Schlaepfer MA, Figueroa-Sandí R. 1998. Female reciprocal calling in a Costa Rican leaf-litter frog, *Eleutherodactylus podiciferus*. Copeia. 1998(4):1076–1080.

Sinsch U, Joermann G. 1989. Vocalization and mating behavior of the marsupial frog, *Gastrotheca marsupiata* (Dumeril and Bibron, 1841) (Amphibia:Hylidae). Copeia. 1989(3):755–760.

Stewart MM, Rand AS. 1991. Vocalizations and defense of retreat sites by male and female frogs, *Eleutherodactylus coqui*. Copeia. 1991(4):1013–1024.

Stewart MM, Rand AS.1992. Diel variation in the use of aggressive calls by the frog *Eleutherodactylus coqui*. Herpetologica. 48(1):49–56.

Toledo LF, Haddad CFB. 2005. Acoustic repertoire and calling behavior of *Scinax fuscomarginatus* (Anura, Hylidae). J Herpetol. 39(3):455–464.

Townsend DS. 1989. The consequences of microhabitat choice for male reproductive success in a tropical frog (*Eleutherodactylus coqui*). Herpetologica. 45(4):451–458.

Townsend DS, Stewart MM. 1986. Courtship and mating behavior of a Puerto Rican frog, *Eleutherodactylus Coqui*. Herpetologica. 42(2):165–170.

Vaira M. 2002. Anurans of a subtropical montane forest in northwestern Argentina: ecological survey and a proposed list of species of conservation concern. Biodivers Conserv. 11:1047–1062.

Vaira M, Ferrari L. 2008. A new species of *Oreobates* (Anura: Strabomantidae) from the Andes of northern Argentina. Zootaxa. 1908:41–50.

Wells KW. 1977. The social behaviour of Anuran Amphibians. Anim Behav. 25: 666–693.

Wells KW. 1981. Territorial behavior of the frog *Eleutherodactylus urichi* in Trinidad. Copeia. 1981(3):726–728.

Wells KW. 1988. The Evolution of the Amphibian Ear. New York: John Wiley. Chapter 20, The effect of social interactions on anuran vocal behavior. p. 433–454.

Wells KW. 2007. The Ecology and Behavior of Amphibians. Chicago: The University of Chicago Press.

Wilczynski W, Brenowitz EA. 1988. Acoustic cues mediate inter-male spacing in a neotropical frog. Anim Behav. 36:1054–1063.

Woolbright LL. 1985. Patterns of nocturnal movement and calling by the tropical frog *Eleutherodactylus coqui*. Herpetologica 41(1):1–19.