ACTA ZOOLOGICA BULGARICA
Acta zool. bulg., 65 (4), 2013: 479-486

Advertisement Calls and Interspecific Variation in *Hypsiboas cordobae* and *Hypsiboas pulchellus* (Anura, Hylidae) from Central Argentina

***Mariana Baraquet*[1,2], *Nancy E. Salas*[1], *Adolfo L. Martino*[1]**

[1] Ecología, Departamento de Ciencias Naturales, Facultad de Ciencias Exactas, Físico-Químicas y Naturales, Universidad Nacional de Río Cuarto. Ruta Nacional N° 36–km 601, (X5804BYA) Río Cuarto, Argentina.

Abstract: The work aims to expand knowledge of the advertisement calls of *Hypsiboas pulchellus* and *Hypsiboas cordobae* from central Argentina. We provide information on each species' calling behaviour, and spectral and temporal features of the advertisement call. Both species presented a characteristic vocalization that allows their taxonomic identification. Discriminant analyses showed differences between the two species in study, with erroneous classification percentages lower than 20% (3.45% for *H. cordobae* and 2.5% for *H. pulchellus*). It could be inferred then that there is low intraspecific variability and high interspecific variation in calls.

Key words: bioacoustics, advertisement call, *Hypsiboas cordobae*, *Hypsiboas pulchellus*, Argentina

Introduction

Acoustic communication is an important feature of anuran social behaviour (Schneider, Sinsch 1992, Pargana *et al.* 2003; Friedl, Klump 2001) and plays an important role in reproductive behaviour (Brenowitz, Rose 1999). In most taxa, males produce advertisement calls to attract conspecific females (Barrio 1964, Brenowitz, Rose 1999, Bosch, de la Riva 2004, Friedl, Klump 2005). These calls constitute the major pre-mating reproductive isolating mechanism in anurans (Gerhardt 1974, Blair 1958). In consequence, the study of vocalization is extensively used to elucidate taxonomic and phylogenetic problems. It is also considered an important character for species identification (Blair 1958, Basso, Basso 1987, Penna, Veloso 1987, Vasara *et al.* 1991, Schneider *et al.* 1993, Márquez *et al.* 1993, Márquez 1995, di Tada *et al.* 1996a, 1996b, Köhler, Lötters 1998, Salas *et al.* 1998, Bosch *et al.* 1999, Guimarães, Bastos 2003, Pombal, Bastos 2003, Bernal *et al.* 2004).

Variation in the advertisement call of a particular anuran species may be due to factors such as air and/or water temperature, size of the calling male, physiological condition, and social context in which the call is emitted (De la Riva *et al.* 1996). Environmental conditions may affect anuran call characteristics (Brenowitz 1986, Bosch, de la Riva 2004) and because of their ectothermic condition, it is expected that the acoustic properties vary with temperature and other climatic variables (Duellman, Trueb 1986). Several studies have demonstrated that environmental factors affect the calls (Vasara *et al.* 1991, Heyer 1994, Martino, Sinsch 2002, Bosch, De la Riva 2004, Bionda *et al.* 2006, Baraquet *et al.* 2007, Bionda *et al.* 2008).

The genus *Hypsiboas* Wagler, 1830 contains 84 species, most of which are included in seven species groups (Frost 2011, Lehr *et al.* 2011). One of them is the *Hypsiboas pulchellus* group, which currently contains 36 species (Frost 2011, Köhler *et al.* 2010, Lehr *et al.* 2010, Lehr *et al.* 2011) including *Hypsiboas pulchellus* (Duméril, Bibron, 1841) and *Hypsiboas cordobae* (Barrio 1965) which are known to inhabit the central area of Argentina.

H. pulchellus, is a widely distributed amphibi-

*Corresponding author: martino@exa.unrc.edu.ar; mbaraquet@exa.unrc.edu.ar

an, that occurs from Santa Catalina to Rio Grande do Sul in Brazil and Uruguay, and Misiones, Corrientes, Entre Ríos, Santa Fe, La Pampa, Chaco, Córdoba, Buenos Aires and northern Río Negro Province in Argentina. Its sister species, *H. cordobae*, is found in Córdoba and San Luis hills (Barrio 1962, 1965, Cei 1980, Gallardo 1974, 1987, Basso, Basso 1987, Basso 1990, Martori, Avila 1992, Bridarolli, di Tada 1994, di Tada *et al*. 1996b, Avila *et al*. 1999, di Tada 1999, Langone , Lavilla 2002, Faivovich *et al*. 2004) but the exact boundaries of its range remain unknown, especially in the contact area with *H. pulchellus* (Barrio 1965, Cei 1980, Gallardo 1987, Bridarolli, di Tada 1994) and the syntopy areas for these species are not known.

Previous studies have addressed spectral and temporal properties of the advertisement calls for these two sister species, and observed differences in advertisement call structure and morphometrics for both species studied (Barrio 1962, 1965, Cei 1980, Basso, Basso 1987, di Tada *et al*. 1996a, Salas *et al.* 1998, Faivovich *et al*. 2004, Baraquet *et al*. 2007). Yet these works are only descriptive, and only the work of Baraquet *et al*. (2007) quantitatively explored the effect of temperature on different call variables. It was therefore necessary to conduct a sampling of advertisement calls at a wide range of temperatures for the application of multivariate statistics to differentiate the species. Also, The IUCN Red List of Threatened Species reports *H. cordobae* as data deficient since it has only recently been removed from synonymy, and there is still very little information on its extent of occurrence, status and ecological requirements, making this species important for study.

In this work we described the spectral and temporal features of the advertisement calls of *H. cordobae* and *H. pulchellus* inhabiting the central area of Argentina. We assessed the temperature influence on several acoustic variables and analysed acoustic differences between both species.

Material and Methods

Advertisement call recordings for *H. cordobae* were obtained in several localities of Cordoba and San Luis provinces and advertisement call recordings for *H. pulchellus* were obtained in three localities of Cordoba province (Table 1), the species being allopatric in all localities.

The fieldwork was conducted during both species reproductive period (from September to May) between 2006 and 2010. The advertisement calls were recorded with a Digital Walkman Audio Tape (DAT) Sony™ TCD-100 with stereo microphone ECM-MS907 Sony™ and TDK™ DAT-RGX 60, at a sampling frequency rate of 44.1 kHz; and air temperature at each calling site was recorded with a digital thermometer (precision = 0.1º C).

The calls were analyzed using Adobe® Audition™ 1.0 (FFT (Fast Fourier transform): 1024 points, 44.1 KHz, resolution 16 bit).

We analyzed 1090 calls from 58 individuals of *H. cordobae* and 1056 calls from 40 individuals of *H. pulchellus*. Each call was characterized by the following parameters: 1. number of notes per call (N/C); 2. call duration (CD); 3. note duration (ND); 4. inter–note interval (IN); 5. inter–call interval (IC); 6. call rate (CR) in calls by minutes (c/m), 7. dominant frequency of the call (DFC), 8. dominant frequency of the note (DFN). Each of these selected calls was filtered to eliminate noise.

We calculated mean, standard deviation, maximum and minimum values for each variable using Statgraphics Plus 5.0. All data were tested for normality of distribution using the Shapiro-Wilks test. The species were compared using the variables shared by all individuals (CD, ND1, ND2, IN1, CR, DFC, DF1, DF2) with parametric one–way ANOVA.

To examine the relationships among advertisement call and temperature we used the residuals from the regression of call variables on air temperature. All variables that were significantly correlated with temperature were standardized to 18°C before further analyses. The temperature standardized call data was analyzed using discriminant analysis. These analyses were performed using Statgraphics Plus 5.0.

Results

Characterization of advertisement calls

A simple basic advertisement call consisting of two–five tonal notes was observed. The final notes of the calls showed longer duration than the first ones.

Both species emitted their calls forming chorus, although some individuals were found vocalizing alone. The call is commonly initiated by a single individual, and others response to it.

The inter–call interval was longer at the beginning and the end of the calls, as well as during individual calling compared with vocalisation in chorus. Therefore, the inter–call interval had a very high standard deviation, because individuals emitted series of calls separated by short intervals, while the series were separated by longer intervals.

Table 1. Latitude, longitude, altitude and provinces of each locality in which the advertisement calls were recorded for each species

Species	Localities	Latitude S Longitude W	Altitude m a.s.l.	Provinces
H. pulchellus	Río Cuarto	33º 06‘ 40.78” 64º 18’ 16.88”	420	Córdoba
	Alejandro Roca	33º 21’ 06” 63º 42 ‘ 10”	206	Córdoba
	Las Acequias	33º 15’ 26.16” 63º 55’ 15.10”	269	Córdoba
H. cordobae	La Carolina	32º 48’ 43.94” 66º 05’ 48.15”	1634	San Luis
	Pampa de Achala	31º 49’ 41.8” 64º 51’ 44.9”	2150	Córdoba
	Achiras	33º 09’ 28.64” 64º 58’ 55.13”	808	Córdoba
	Las Guindas, Alpa Corral	32º 35’ 35.22” 64º 42’ 38.92”	930	Córdoba
	Los Tabaquillos	32º 23’ 59.75” 64º 55’ 33.69”	2107	Córdoba
	Los Linderos	32º 00’ 54.05” 64º 56’ 42.97”	2310	Córdoba

In both species we observed the presence of a simple tonal sound that was alternated with calls.

Hypsiboas cordobae

Specimens of this species were observed vocalizing at water bodies edges (rivers, streams), on stones or vegetation (on aquatic plants or higher plants, one meter tall). The individuals partly submerged in water among aquatic vegetation were also observed calling.

The results showed three types of advertisement calls consisting of three, four and five notes, respectively. The individuals alternated different types of calls, of which the following can be distinguished: 1. individuals calling with only four notes; 2. individuals calling with four notes alternating with five–note calls; 3. individuals calling with four notes alternating with three–note calls; 4. individuals calling with three, four and five notes alternated (Fig. 1, A); and 5. individuals showing only three notes per call.

In percentages, we found 65.23% (711 calls) of four–note calls, 22.57% (246 calls) of three–note calls, 10.46% (114 calls) of five–note calls, and 1.74% (19 calls calls) of two–note calls.

From the 60 individuals studied, 21 individuals presented calls of only four notes and only a single individual presented calls of three notes. There were 19 individuals that presented four–note calls alternating with three–note calls, and six individuals showed calls of four notes alternating with five–note calls. There were also 13 individuals that presented alternating calls of three, four and five notes. Finally, eight individuals presented calls of two notes: five of them alternated calls of two, three, four and five notes, and the other three alternated calls of two, three and four notes.

The three types of calls differed in duration. The final notes were longer than the others, that had a similar average duration (Table 2). In some cases, however, the final notes presented a similar or lower duration than the others.

The calls had a dominant frequency between 1160 and 2450 Hz with a slight increase from the first to the last dominant frequency of each note.

The average duration of inter–call interval was 1310 ± 1252.5 ms, with a range of 146–9748 ms. There was a high variability in this parameter. This was also observed in the call rate (CR), which average was 30.8 c/m (10–81 c/m).

We analyzed 63 simple tonal sounds from 20 individuals, with an average duration of 124.52 ms (182–543), and a dominant frequency within the range of 802.31–2196 Hz. The duration of these sounds was greater than the duration of call notes from the same individual, but the frequencies were always lower.

Hypsiboas pulchellus

Specimens of this species were also observed vocalizing at the edge of water bodies (rivers or gaps), on stones or on vegetation (aquatic plants or higher plants, one meter tall). The individuals of this

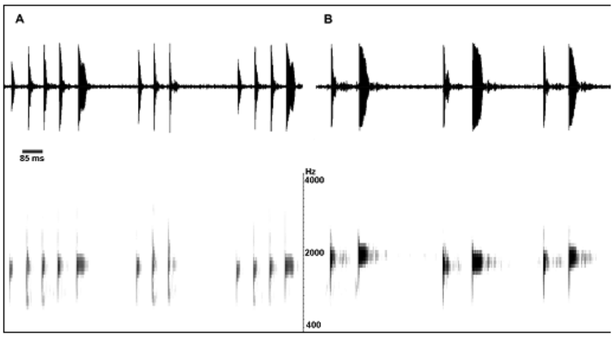

Fig. 1. Oscillogram (above) and sonogram (below) of the advertisement call in (A) *H. cordobae* and (B) *H. pulchellus*

species were observed calling within gaps, on vegetation up to 20 cm from the base, or on aquatic vegetation in contact with water. In this species, there were no records of calls of individuals partly submerged in water.

The results obtained revealed one basic advertisement call formed by two notes (Fig.1, B). We also found individuals with one–note calls alternating with two–note calls, but in very low proportion, only 1.99% (21 calls out of 1056 analyzed).

As in *H. cordobae*, the final notes of *H. pulchellus* were longer; the second note was longer than the first one (Table 3). The calls had a dominant frequency between 1503 and 2756 Hz, with an average frequency of 2331.99 Hz. The dominant frequency of the second note (2345.24 ± 207.013 Hz) was greater than the dominant frequency of the first one (2212.89 ± 273.287 Hz).

The average value of inter–call interval was 291.33 ± 136.28 ms, with a range of 154–504 ms. The call rate presented a range of 34–211 c/m, with an average of 95.08 c/m.

We analyzed 16 simple tonal sounds from 11 individuals, with an average duration of 71.38 ms (43–105 ms), and a dominant frequency between 1392.2 and 2300 Hz. The duration of these sounds was greater than the call notes from the same individual, but the frequencies were always lower.

Acoustic differences between *H. cordobae* and *H. pulchellus.*

The most remarkable difference between both species was the number of notes per call, *H. cordobae* presented calls composed by two, three, four and five notes, whereas *H. pulchellus* presented calls composed by only two notes (Fig. 2).

In both species the call types differed in duration, but the final notes were longer than the first ones. However, some individuals of *H. cordobae* presented similar or lower duration in the final notes.

The two–note call of *H. cordobae* was the most similar to the call of *H. pulchellus*. However, the dominant frequency average values were higher for *H. pulchellus* than for *H. cordobae*.

All of them showed significant differences ($p < 0.05$) when compared via one–way ANOVA (CD $p = 0.0000$, $F = 108.29$; ND1 $p = 0.0006$, $F = 12.64$;

Table 2. Mean and standard deviation values of the acoustic variables analysed for the types of call in *H. cordobae*

Variables	Calls of two notes	Calls of three notes	Calls of four notes	Calls of five notes
CD	116.68 ± 16.02	206.03 ± 34.15	309.94 ± 46.09	354.43 ± 47.74
ND1	17.32 ± 4.97	24.43 ± 11.99	26.91 ± 10.10	20.50 ± 7.48
IN1	54.58 ± 12.24	52.89 ± 17.85	66.91 ± 17.76	61.15 ± 12.17
ND2	42.42 ± 10.83	26.09 ± 11.56	25.12 ± 9.89	20.67 ± 5.44
IN2		48.72 ± 14.85	57.03 ± 16.17	53.88 ± 11.22
ND3		50.26 ± 10.82	27.83 ± 10.63	23.39 ± 6.92
IN3			51.03 ± 15.65	48.90 ± 9.58
ND4			51.81 ± 10.92	27.34 ± 9.50
IN4				48.87± 10.37
ND5				46 ± 9.12
DFC	1911.92 ± 271.45	1812.68 ± 258.30	1865.10 ± 259.13	1691 ± 308.87
DF1	1830.76 ± 253.96	1728.36 ± 256.55	1769.18 ± 219.21	1563.60 ± 264.85
DF2	1944.88 ± 274.90	1784.03 ± 242.55	1800.57 ± 230.43	1590.03 ± 278.42
DF3		1855.4 ± 242.66	1844.12 ± 244.97	1648.65 ± 295.47
DF4			1888.42 ± 253.51	1693.64 ± 300.79
DF5				1726.38 ± 291.22

Table 3. Mean and SD values of the acoustic variables analysed for the types of call in *H. pulchellus*

Variables	Calls of one note	Calls of two notes
CD	38.62 ± 12.86	132.91 ± 31.47
ND1		16.59 ± 4.96
IN1		77.26 ± 31.07
ND2		37.32 ± 6.85
DFC	2162.22 ± 305.02	2331.99 ± 213.94
DF1		2212.89 ± 273.29
DF2		2345.24 ± 207.01

ND2 p = 0.0000, F = 50.96; IN1 p = 0.0000, F = 31.26; CR p = 0.0000, F = 38.79; DFC p = 0.0000, F = 48.08; DFN1 p = 0.0000, F = 55.34; DFN2 p = 0.0000, F = 80.64).

The simple regression analyses showed that all variables vary with temperature (CD: r = -0.623553, R^2 = 38.88%, p = 0.0000; ND1: r = -0.510688, R^2 = 26.08%, p = 0.0000; ND2: r = 0.226563, R^2 = 5.13%, p = 0.0241; IN1: r = -0.289896, R^2 = 8.40%, p = 0.0036; CR: r = 0.561101, R^2 = 31.48%, p = 0.0000; DFC: r = 0.298911, R^2 = 8.93%, p = 0.028; DF1: r = 0.264205, R^2 = 6.98%, p = 0.0082; DF2: r = 0.364726, R^2 = 12.40%, p = 0.0002).

The discriminant analysis yielded one function with an eigenvalue of 2.53 that explained 100% of the observed variation (p = 0.0000). The canonical correlation of 0.85 (close to 1) indicated that the function had a high weight, while the Wilks Lambda of 0.28 (close to 0) indicated that the two selected variables (CD and IN1) were appropriate to discriminate species (Fig. 3). The percentage of cases correctly classified was 96.94% (96.55% for *H. cordobae* and 97.50% for *H. pulchellus*).

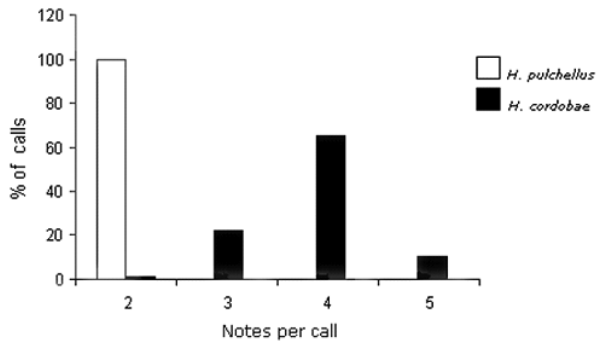

Fig. 2. Types of advertisement calls in each species, and percentage of calls of two, three, four and five notes, respectively.

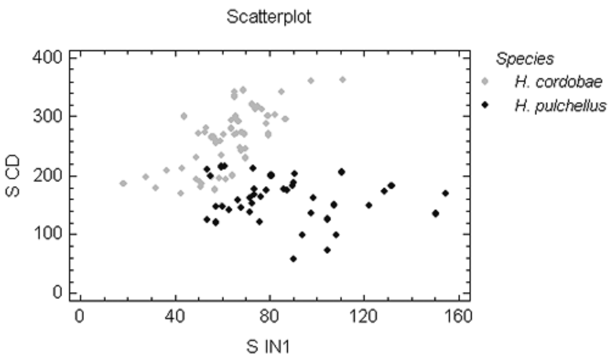

Fig. 3. Discriminant plot showing the standardized variables of greater contribution. S CD: standardized call duration; S IN1: standardized inter–note interval.

Discussion

Several authors have already observed differences in advertisement call structure and morphometrics for both species studied, *H. pulchellus* and *H. cordobae* (Barrio 1965, Basso, Basso 1987, di Tada *et al.* 1996a, Faivovich *et al.* 2004). However, there were no previous attempts to quantitatively explore the effect of temperature on different call related variables, and both species were never compared by multivariate statistical methods.

The results of this study coincided with previous descriptions of advertisement calls in *H. pulchellus* and *H. cordobae*, which were characterized as basic tonal calls formed by two to five series of notes, with the final ones of longer duration. Besides, the individuals of both species emitted their calls individually or forming choirs (Barrio 1962, 1965, Cei 1980, Basso, Basso 1987, di Tada *et al.* 1996a, Salas *et al.* 1998).

The individuals of both species were observed calling out of water, on vegetation or rocks. The individuals of *H. cordobae* were also observed calling partially submerged in water among aquatic vegetation. This behaviour was also described by Barrio (1965) and Gallardo (1987).

Moreover, both species are characterized by the emission of a single sound, different from the typical call notes. This sound (Barrio 1962, 1965) is emitted just once or several times when the individual begins its call. However, we observed that this note was also performed between calls or at the end of calls. This sound has duration of 130 ms (Barrio1962), which is consistent with our results for *H. cordobae* (124.52 ms), but it is higher than the mean duration we observed for *H. pulchellus* (71.38 ms).

We distinguished three different calls for *H. cordobae* composed of three, four and five notes per call, and only one call formed by two notes for *H. pulchellus*. Both species calls differed significantly in duration and dominant frequency. Our results are in agreement with several authors' description of both *H. pulchellus* (Barrio 1962, 1965, Cei 1980, García *et al*. 2003, Baraquet *et al.* 2007) and *H. cordobae* advertisement calls (Barrio1965, Cei 1980, di Tada *et al.* 1996a). However, Basso, Basso (1987) indicated that the call of *H. pulchellus* consists of four notes distributed in two groups. Our results do not show that structure, we basically found a two–note call in this species. Both Barrio (1965) and di Tada *et al.* (1996a) observed calls of three and four notes for *H. cordobae*, while in this work we also found calls with five notes.

Calls comprised of one note for *H. pulchellus* and of two notes for *H. cordobae*, which differ from the basic pattern for both species, are consistent with reports by other authors indicating that call can be modified in different ways (Barrio 1965, Vasara *et al*. 1991, Márquez *et al*. 1993, Baraquet *et al*. 2007).

In both species calls, the final note was the longest and the three–note call of *H. cordobae* was the most similar to that of *H. pulchellus*.

The bioacoustic variables of the advertisement call in *H. pulchellus* (call duration, duration of the first note, duration of the second note and dominant frequency of the call) were similar to those presented by Barrio (1962, 1965), Salas *et al*. (1998) and Baraquet *et al*. (2007).

The description and values of advertisement call obtained in this work for *H. cordobae* are in agreement with values reported by di Tada *et al*. (1996a). However, the duration of the third and fourth notes as well as the dominant frequency range reported by those authors were lower compared to values obtained in this work.

The dominant frequency of the call and that of each note were higher in *H. pulchellus* in comparison with *H. cordobae.* This difference is consistent with differences in body size between species; *H. cordobae* is slightly larger than *H. pulchellus* (Cei 1980, Gallardo 1987). The frequency of anuran acoustic signals is partially determined by the shape and mass of the laryngeal apparatus, which is in turn related to body size (Duellman, Trueb 1986). Therefore, an increase in the vocal cords cartilage and in the soundboard will produce deeper and lower frequency sounds (Bernal *et al.* 2004).

Many studies report that male size is highly and negatively correlated with the dominant frequency of the advertisement call (Sullivan *et al.* 1996, Bee *et al.* 2000, Bosch *et al.* 2000, Gerhardt 1994, Burmeister *et al.* 1998, Bee, Gerhardt 2001, Bernal *et al*. 2004).

Intra and interspecific variation was observed in inter–note interval and call rate. Several authors have shown that male frogs can change some characteristics of their call to reflect the social context within which they are calling (Schwartz 1989, Burmeiter *et al*. 1999, Bernal *et al*. 2004), and that the most common response of males to other competing males is an increase in the call rate. Thus, when individuals call alone, especially when they begin to vocalize, the call rate is low, whereas when they call in chorus the call rate increases significantly (Schwartz, Wells 1985, Bosch *et al*. 2000, Bosch, de La Riva 2004, Bernal *et al*. 2004, Bernal *et al*. 2007). Bernal *et al*. (2004) attributed these variations to a strategy of males to avoid overlap and interferences of the calls, and thus, females consistently select the alternative with high call repetition rate (Schwartz, Wells 1985, Bosch, Marquez 2005). This could explain the fact that in both species the inter–call interval was longer at the beginning and at the end of their calls, as well as during individual calling compared with vocalisation in chorus.

However, other factors seem to affect all these acoustic parameters. Ziegler *et al*. (2011) identified a plausible causal structure connecting environment, individual attributes, and temporal and spectral adjustments as direct or indirect determinants of the observed variation in call attributes of *Hypsiboas pulchellus*. These authors revealed a strong effect of the habitat structure on the temporal parameters of the call, and suggested the effects of local vegetation, temperature and proportion of water in the environment as determinants of the temporal variables. In addition, the mentioned authors showed that the spectral variables were related only to the size of the calling males, and explained this as an effect of the site temperature that determined the size of organisms calling at each site and thus indirectly affecting the dominant frequency of the call. In summary, the two main determinants of the call attributes: On the one hand, environmental conditions consistently affect temporal attributes, and on the other hand, individual attributes affect the spectral structure of calls; the males of *H. pulchellus* have the potential to adjust their calls in response to their local environment.

The discriminant analysis allowed us to differentiate the two species with a highly significant function. The percentage of the correctly classified cases was high in both species. Schneider, Sinsch (1992) considered these classification percentages as a quantitative measure for the local variability in advertisement calls, which can be distinguished from taxonomic differences among populations. In addition, they stated that erroneous classification rates below 20% were evidence of random variation. We obtained classification percentages lower than 20% (3.45% and 2.5% for *H. cordobae* and *H. pulchellus*, respectively). We could say then that there is an evidently low intraspecific variability and a high interspecific variation in the advertisement calls.

The results obtained here show that the two species have common features, thus reflecting their phylogenetic proximity (Faivovich *et al.* 2004, Faivovich *et al.* 2005). However, because the anuran call is an effective mechanism for pre–reproductive isolation and is therefore useful for species identification (Duellman, Trueb 1986, di Tada *et al.* 1996a), our results also show differences in the advertisement call of both species.

Its characterization and variability, coupled with the many factors that may affect it are then valuable information for taxonomic, phylogenetic and ecological approaches.

Acknowledgements: The first two authors thank the National Scientific and Technical Research Council (CONICET) for the support. The Secretary of Science and Technology of National University of Río Cuarto (SECyT-UNRC) provided funds under Grant PPI 18C/225. We thank J. Valetti for the help in the field and sampling. Our study was authorized by the Cordoba Environmental Agency (A.C.A.S.E.).

References

Avila L. J., M. Morando and J. M. Priotto 1999. Amphibia and Reptilia of the high grasslands of the Sierra de Comechingones, Córdoba, Argentina. – *Bulletin of the Maryland Herpetological Society. Department of Herpetology the Natural History Society of Maryland inc.*, **35**: 97-113.

Baraquet M., N. E. Salas and I. E. di Tada 2007. Variación geográfica en el canto de advertencia de *Hypsiboas pulchellus* (Anura, Hylidae) en Argentina. – *Revista Española de Herpetología*, **21**: 107-118.

Barrio A.1962. Los Hylidae de Punta Lara, Provincia de Buenos Aires. Observaciones sistemáticas, ecológicas y análisis espectrográfico del canto. – *Phycis*, **23**: 129-142.

Barrio A. 1964. Importancia, significación y análisis del canto de batracios anuros. – *Publicación Museo Provincial Ciencias Naturales "F. Ameghino", Santa Fe*, 51-79.

Barrio A. 1965. Las subespecies de *Hyla pulchella* Duméril & Bibron (Anura, Hylidae). – *Phycis*, **25**: 115-128.

Basso N. G. 1990. Estrategias adaptativas en una comunidad subtropical de anuro. – *Cuadernos de Herpetología*, *Serie monografías* Nº 1.

Basso N. G., G. Basso 1987. Análisis acústico del canto de *Hyla pulchella pulchella* (Duméril & Bibron, 1841) (Anura: Hylidae). – *Anales Museo de Historia Natural*, **18**: 109-114.

Bee M. A., C. Gerhardt 2001. Neighbour–stranger discrimination by territorial male bullfrogs (*Rana catesbeiana*): I. Acoustic basis. – *Animal Behaviour*, **62**: 1129-1140.

Bee M A., S. A. Perrill and P. C. Owen 2000. Male green frogs lower the pitch of acoustic signals in defense of territories: a possible dishonest signal of size? – *Behavioral Ecology*, **11**: 169-177.

Bernal M. H., D. P. Montealegre and C. A. Paez 2004. Estudio de la vocalización de trece especies de anuros del municipio de Ibagué, Colombia. – *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, **28**: 385-390.

Bernal X. E., A. S. Rand and M. J. Ryan 2007. Sex differences in response to nonconspecific advertisement calls: receiver permissiveness in male and female túngara frogs. – *Animal Behaviour*, **73**: 955-964.

Bionda C., N. Salas and I. Di Tada 2006. Variación bioacústica en poblaciones de *Physalaemus biligonigerus* (Anura: Leptodactylidae) en Córdoba, Argentina. – *Revista Española de Herpetología*, **20**: 95-104.

Bionda C., N. Salas and I. Di Tada 2008. Effect of temperature on the advertisement call of *Physalaemus bilingonigerus* (Anura: Leptodactylidae). *Boletín de la – Asociación Herpetológica Española*, **19**: 19-22.

Blair W. F. 1958. Mating call in the speciation of anuran amphibians. – *The American Naturalist*, **92**: 27-51.

Bosch J., I. De la Riva and R. Márquez 1999. Advertisement calls of seven species of hyperoliid frogs, from Equatorial Guinea. – *Amphibia-Reptilia*, **21**: 246-255.

Bosch J., A. S. Rand and M. J. Ryan 2000. Acoustic competition in *Physalaemus pustulosus*, a differential response to calls of relative frequency. – *Ethology*, **106**: 865-871.

Bosch J., I. De la Riva. 2004. Are frog calls modulated by the environment? An analysis with anuran species from Bolivia. – *Canadian Journal of Zoology*, **82**: 880-888.

Bosch J., R. Márquez 2005. Female preference intensities on different call characteristics and symmetry of preference above and below the mean in the Iberian Midwife Toad *Alytes cisternasii*. – *Ethology*, **111**: 323-333.

Bridarolli M. E., I. E. di Tada 1994. Biogeografía de los Anfibios Anuros de la Región Central de la República Argentina. – *Cuadernos de Herpetología*, **8**: 63-82.

Brenowitz E. A. 1986. Environmental influences on acoustic and electric animal communication. – *Behavior and Evolution*, **28**: 32-42.

Brenowitz E. A., G. J. Rose 1999. Female choice and plasticity of male calling behaviour in the Pacific treefrog. – *Animal Behaviour*, **57**: 1337-1342.

Burmeister S., W. Wilczynski and M. J. Ryan 1998. Temporal call changes and prior experience affect graded signalling in the cricket frog. – *Animal Behaviour*, **57**: 611-618.

Cei J. M. 1980. Amphibians of Argentina. Monitore Zoologico Italiano (Nuova Serie), Monographs, Firenze.

De la Riva I., R. Márquez and J. Bosch 1996. Advertisement calls of four Microhylid Frogs from Bolivia (Amphibia, Anura). – *The Amercian Midland Naturalist*, **136**: 418-422.

Di Tada I. E. 1999. Patrones de distribución de los anfibios anuros de la provincia de Córdoba. Tesis Doctoral presentada en la Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba.

Di Tada I. E., M. V. Zavattieri and A. L. Martino 1996a. Análisis estructural del canto de *Hyla pulchella cordobae* (Amphibia: Hylidae) en la provincia de Córdoba (Argentina).

– *Revista Española de Herpetología*, **10**: 7-11.

Di Tada I. E., M. V. Zavattieri, N. E. Salas and A. L. Martino 1996b. Anfibios Anuros de la provincia de Córdoba. – In: di Tada I. E., Bucher E. H (Eds): Biodiversidad de la provincia de Córdoba. Volumen I. Fauna. Río Cuarto (Universidad Nacional de Río Cuarto), **1**: 191-213.

Duellman W. E., L. Trueb 1986. Biology of Amphibians. USA (McGraw Hill Inc.). 670 p.

Faivovich J., P. C. A. García, F. Ananias, L. Lanari, N. G. Basso and W. C. Wheeler 2004. A molecular perspective on the phylogeny of the *Hyla pulchella* species group (Anura, Hylidae). – *Molecular Phylogenetics and Evolution*, 32: 938-950.

Faivovich J., C. F. B. Haddad, P. C. A. García, D. R. Frost, J. A. Campbell and W. C. Weeler 2005. Systematic review of the frog Family Hylidae, with special reference to Hylinae: Phylogenetic analysis and taxonomic revision. – *Bulletin of American Museum of Natural History New York*, **294**: 1-240.

Friedl T. W. P., G. M Klump. 2001. The vocal behaviour of male European treefrogs (*Hyla arborea*): implications for inter- and intrasexual selection. – *Behaviour*,**139**: 113-136.

Friedl T. W. P., G. M. Klump 2005. Sexual selection in the lek-breeding European treefrog: body size, chorus attendance, random mating and good genes. – *Animal Behaviour*, **70**: 1141-1154.

Frost D. R. 2011. Amphibian Species of the World: an Online Reference. Version 5.5. Available from: http://research.amnh.org/herpetology/amphibia/index.php. American Museum of Natural History, New York, USA.

Gallardo J. M. 1974. Anfibios de los alrededores de Buenos Aires. Buenos Aires (Editorial Universitaria de Buenos Aires). 231 p.

Gallardo J. M. 1987. Anfibios Argentinos. Guía para su identificación. Buenos Aires (Biblioteca Mosaico, Lib. Agropecuaria). 98 p.

García P. C. A., G. Vinciprova and C. F. B. Haddad 2003. The taxonomic status of *Hyla pulchella joaquini* (Anura: Hylidae) with description of its tadpole and volcalization. – *Herpetologica,* **59**: 350-363.

Gerhardt H. C. 1974. The significance of some spectral features in mating call recognition in the green treefrog *Hyla cinerea*. – *Journal of Experimental Biology*, **61**: 229-241.

Gerhardt H. C. 1994. The evolution of vocalization in frogs and toads. – *Annual Review in Ecology and Systematics*, **25**: 293-324.

Guimarães L. D., R. P. Bastos 2003. Vocalizações e interações acústicas em *Hyla raniceps* (Anura, Hylidae) durante a atividade reprodutiva. – *Iheringia, Série Zoológica*, **93**: 149-158.

Heyer W. R. 1994. Variation within the *Leptodactylus podicipinus-wagneri* complex of frogs (Amphibia: Leptodactylidae). – Smithsonian Contributions to Zoology, **546**: 1-124.

Köhler J., S. Lötters 1998: Advertisement calls of two Bolivian *Leptodactylus* (Amphibia: Anura: Leptodactylidae). – *Amphibia-Reptilia*, **20**: 215-219.

Köhler J., D. Koscinski, J. M. Padial, J. C. Chaparro, P. Handford, S. C. Lougheed and I. De La Riva 2010. Systematics of Andean gladiator frogs of the *Hypsiboas pulchellus* species group (Anura, Hylidae). – *Zoologica Scripta*, 1-19.

Langone J. A., E. O. Lavilla 2002. Comentarios nomenclatoriales sobre algunos taxa del grupo de *Hyla pulchella* (Anura: Hylidae). – *Cuadernos de Herpetología*, **16**: 73-78.

Lehr E., J. Faivovich and K. H. Jungfer 2010. A new Andean species of the *Hypsiboas pulchellus* group: adults, calls and phylogenetic relationships. – *Herpetologica*, 66: 296-307.

Lehr E., J. Faivovich and K. H. Jungfer 2011. Description of the tadpoles of *Hypsiboas aguilari* and *H. melanopleura* (Anura: Hylidae: *Hypsiboas pulchellus* group). – *Salamandra*, **47**: 30-35.

Márquez R., I. De La Riva and J. Bosch 1993. Advertisement calls of Bolivian species of *Hyla* (Amphibia, Anura, Hylidae). – *Biotropica*, **25**: 426-443.

Márquez R. 1995. Preferencias de las hembras por cantos de frecuencia dominante baja en el sapo partero común *Alytes obstetricans* (Anura, Discoglossidae). Experimentos *in situ.* – *Revista Española de Herpetología*, **9**: 77-83.

Martino A. L., U. Sinsch 2002. Speciation by polyploidy in *Odontophrynus americanus*. – *Journal of Zoology (London)*, **257**: 67-81.

Martori R., L. J. Avila 1992. Confirmación de la Presencia de *Hyla pulchella pulchella* para la Provincia de Córdoba (Argentina). – B*oletín Asociación Herpetológica Argentina*, **8**: 4–5.

Pargana J. M., R. Márquez, R. Reuqes, M. J. Sánchez-Herraiz, M. Tejedo and E. G. Crespo 2003. The mating call of *Pelodytes ibericus* (Anura, Pelodytidae). – *Herpetological Journal*, **13**: 199-204.

Penna M., A. Veloso 1987. Vocalization by andean frogs of the genus *Telmatobius* (Leptodactylidae). – *Herpetológia*, **43**: 208-216.

Pombal J. P., R. P. Bastos 2003. Vocalizações de *Scinax perpusillus* (A. Lutz & B. Lutz) e *S. arduous* Peixoto (Anura, Hylidae), com comentários taxonômicos. – *Revista Brasileira de Zoologia*, **20**: 607-610.

Salas N. E., M. V. Zavattieri, I. E. Di Tada, A. L. Martino and M. E. Bridarolli 1998. Bioacustical and etho-ecological features in amphibian communities of southern Córdoba province (Argentina). – *Cuaderno de Herpetología*, **12**: 37-46.

Schneider H., U. Sinsch 1992. Mating call variation in lake frogs referred to as *Rana ridibunda* Pallas, 1771. – *Zeitschrift fuer zoologische Systematik und Evolutionsforschung*, **30**: 297-315.

Schneider H., U. Sinsch and T. S. Sofianidou 1993. The water frog of Greece. Bioacoustic evidence for a new species. – *Zeitschrift fuer zoologische Systematik und Evolutionsforschung*, **31**: 47-63.

Schwartz J. J. 1989. Graded aggressive calls of the spring peeper, *Pseudacris crucifer*. – *Herpetologica*, **45**: 172-181.

Schwartz J. J., K. D. Wells 1985. Intra- and interspecific vocal behavior of the Neotropical Treefrog *Hyla microcephala*. – *Copeia*, **1**: 27-98.

Sullivan B. K., K. M. Malmos and M. F. Given 1996. Systematics of the *Bufo woodhousii* complex (Anura: Bufonidae): Advertisement call variation. – *Copeia*, **2**: 274-280.

Vasara E., T. S. Sofianidou and H. Schneider 1991. Bioacustic analysis of the Yellow-bellied Toad in Northern Greece (*Bombina variegata scabra* L., Anura, Discoglossidae). – *Zoologischer Anzeiger*, **226**: 220-236.

Ziegler L., M. Arim and P. M. Narins 2011. Linking amphibian call structure to the environment: the interplay between phenotypic flexibility and individual attributes. – *Behavioral Ecology*, **22**: 520-526.

Received: 15.07.2011
Accepted: 21.09.2012