Vocal patterns of adult females and juveniles *Caiman yacare* (Crocodilia: Alligatoridae) in Brazilian Pantanal wetland

Fernando L. Sicuro*[1], Gilson E. Iack-Ximenes[2], Henrique Wogel[3] & Marcos Bilate[4]

1. BioVasc, Departamento de Ciências Fisiológicas, Universidade do Estado do Rio de Janeiro, 20550-013, Maracanã, Rio de Janeiro, Brazil; fsicuro@gmail.com
2. Departamento de Ciências Naturais, Universidade Estadual do Sudoeste da Bahia, 45083-900, Vitória da Conquista, Bahia, Brazil; giliack@gmail.com
3. Curso de Ciências Biológicas, Escola de Ciências da Saúde, Universidade do Grande Rio, 25071-202, Duque de Caxias, Rio de Janeiro, Brazil; hwogel@gmail.com
4. Seção de Herpetologia, Museu Nacional, Universidade Federal do Rio de Janeiro, 20940-040, Quinta da Boa Vista, Rio de Janeiro, Brazil; marcosbilate@gmail.com

* Correspondence

Received 30-VII-2012. Corrected 10-I-2013. Accepted 24-I-2013.

Abstract: Patrones de vocalización de jóvenes y hembras adultas de *Caiman yacare* (Crocodilia: Alligatoridae) en el Pantanal de Brasil. The Paraguayan caiman (*Caiman yacare*) is the main Caimaninae species occurring in the Brazilian Pantanal Wetland. Despite the relative availability of works focused on biology and conservation of the Paraguayan caiman, almost nothing is known about its vocal structure and behavior. We recorded aggressive calls of adult caiman females guarding nests and, afterwards, the distress calls of the new born juvenile caimans in seasonally flooded areas of the Nhecolândia (Southern Pantanal). The results of both observations and sonographic analyses diverged from studies with other crocodilian species. Aggressive vocalization of adult females of the Paraguayan caiman was longer and more complex than the same vocalization of larger Alligatoridae species. Vocalizations of the young caimans presented interspecific differences with other crocodilian offsprings. Moreover, we found statistically significant intraspecific variation in the distress call structure among different pods, even separated by few kilometers. Differences in distress call structure were tested by Canonical Discriminant Analysis (CDA). We obtained the squared Mahalanobis distances between the acoustic multivariate spaces of each pod provided by the CDA and compared with the geographic distance between the bays of origin of each pod through Mantel Test. The geographic distance by itself did not explain the differences found in the structure of the vocalization of young caimans from different pods. The adult females of Paraguayan caiman positively responded to playbacks of calls from juvenile caimans from pods of other regions, as well as to rough imitations of distress call. Since the adult caimans showed protective responses to quite heterogeneous vocalizations of distress by juveniles, we hypothesized that the variation in the distress call pattern may be associated to a low specificity in sound recognition by adult caimans. Rev. Biol. Trop. 61 (3): 1401-1413. Epub 2013 September 01.

Key words: Paraguayan caiman, Caimaninae, distress call, vocalization, parental care, sonogram, statistical multivariate methods.

Complex social signs and behavioral displays are present in all genera of the order Crocodilia. Crocodilians feature high vocal and hearing capacities and their sexual and parental interactions are marked by different vocalizations (Wever 1971, Vergne & Mathevon 2008, Benko & Perc 2009, Wang *et al.* 2009a, 2009b). Variation in vocal patterns as behavioral responses to environmental stimuli have been observed in crocodilians at all stages of ontogenetic development (Campbell 1973, Hunt & Watanabe 1982, Vliet 1989).

Young and adult crocodilians present marked vocal differences related to ontogenetic variations. These are associated to the individual size, shape and physiological parameters that affect the sound waves frequency and, consequently, the tone (Fitch 1997, Bond & Diamond 2005). Vocalizations in crocodiles are produced through air pressure in vocal folds of the larynx. Two parameters can alter the modulate frequency in crocodiles: subglottal pressure and vocal fold adduction (Riede *et al*. 2011). Ontogenetic differences related to vocal folds development will affect sound production. Modulation in frequency parameters explains the main differences in the vocal repertoire among adult and young caimans. As vocal fold length is positively correlated with body mass (Fitch 2000, Riede & Titze 2008, Riede *et al.* 2011), ontogenetic size differences will affect sound production and vocal repertoire (Riede *et al*. 2011).

Adult males vocalize and display body postures during territorial contests and adult females emit aggressive vocalizations while guarding nests (Brazaitis 1973, Garrick *et al.* 1978, Magnusson 1980, Vliet 1989). Adult crocodilian females show parental care by guarding their nests and demonstrating aggressive displays, including vocalizations and attempts to attack, when intruders are nearby the nesting area (Stanton 1978, Crawshaw & Schaller 1980, Ayarzagüena 1983, Cintra 1988).

At hatching, young crocodilians vocalize within the egg and nest to attract adults to release them (Crawshaw & Schaller 1980, Magnusson 1980, Vergne & Mathevon 2008). After the formation of creches, the vocalization is the main factor of cohesion between the young crocodilian and its pod (group of young of similar age), and their contact with the adults. Furthermore, young crocodilians emit loud-pitched calls in stress situations, called distress calls, which are interpreted as a defensive behavior. Juvenile calls can be used to attract adult attention (not necessarily the parents) for protection, and alarm other pod members to a potential danger (Stanton 1978, Romero 1983, Gorzula 1985, Allsteadt & Vaughan 1988).

The genus *Caiman* Spix, 1825 is currently composed of three species: *Caiman crocodilus* (Linnaeus, 1758), *C. latirostris* and *C. yacare* (Daudin, 1802). Brochu (1999) included *Caiman* along with other Neotropical caimans (*e.g. Paleosuchus*, *Melanosuchus*) in the Caimaninae (Alligatoridae). Caimaninae is a monophyletic group strongly supported by morphological and molecular analysis (Brochu 1999, Oaks 2011).

The Paraguayan caiman, *C. yacare*, occurs from Amazonia to the Pantanal Wetland transition. Their distribution includes Mamoré, Guaporé, Paraguay and Paraná river systems and all of their lowland drainages. This area includes parts of Central-Western Brazil, Eastern Paraguay, and Southeastern Bolivia (Brazaitis *et al.* 1998, Campos *et al.* 2010). Busack & Pandya (2001), using discriminant function analysis based on 13 morphological characters, pointed out that the individuals from these localities consistently differentiate *C. yacare* from subspecies of *Caiman crocodilus*. Formerly, Brochu (1999) recognized a well-supported clade composed by *C. yacare* and *C. crocodilus* in Caimaninae and distinguished *C. yacare* by the midline contact between the prefrontal. Nevertheless, Hrbek *et al.* (2008) studying specimens from the upper Madeira River suggest no genetic support to consider *C. yacare* distinct from *C. crocodilus*. Hrbek *et al*. (2008) and Velasco & Ayarzagüena (2010) concluded that the phylogenetic and taxonomic relationships between *C. crocodilus* and *C. yacare* remain inconclusive.

In this present study we follow the current taxonomic arrangement for *Caiman* (Escobedo-Galvan *et al.* 2011) and we considered the Paraguayan caiman as a full species as proposed by King & Burke (1989). However, we stress the strong phylogenetic relationship with *Caiman crocodilus* complex as pointed out by several authors (Brazaitis *et al.* 1998, Busack & Pandya 2001, Hrbek *et al.* 2008, Martin 2008).

Despite the relative availability of works focused on the biology and conservation of the Paraguayan caiman, almost nothing is known about its vocal structure and behavior, hitherto.

This study aims to analyze the vocalization structure of adult female *C. yacare* during nest guarding and when young caimans are emitting distress calls in the following weeks after their hatch. The distances between the sites of recordings were taken into account to assess the variation between the call structures of juvenile pods. We also compared our findings with vocalizations of adult and juvenile individuals of other species of Crocodilia (with emphasis on Alligatorinae species) based on descriptions available in the literature. Some inferences about the responses of adult caimans to playbacks of distress call of juvenile individuals were also made.

MATERIALS AND METHODS

Study site: The Brazilian Pantanal Matogrossense is a large continental savanna wetland covering an area of 147 574km^2 (Alho *et al.* 1988, Alho 2008). This study took place in the Nhecolândia sub-region of Brazilian Pantanal wetland. The Nhecolândia landscape is characterized by a mosaic of semi-deciduous and xeric vegetation, seasonally flooded grasslands and hundreds of small temporary/permanent lakes and ponds (Alho 2008). The data were collected within the Nhumirim research farm (18°59'17" S - 56°37'8.39" W, with *ca* 4350ha of area), on February and April 1992.

Vocalization recording: The vocalizations of female caimans were recorded in February, the time of egg incubation and nest guarding. The distress calls of young caimans were recorded in April, when newborn caimans are gathered in pods (Crawshaw & Schaller 1980, Cintra 1988). Vocalizations were recorded with tape recorder Uher 4 000 Report-L (speed 19.05cm/s), Uher dynamic microphone M 514 (frequency range 70Hz-14 000Hz), and magnetic tape Scotch 1 800-7 Dynarange (6.35mm). The average distance from the microphone to adult caimans was 150cm and 25cm to the young ones. The recordings were edited with Uher 4 200 Record Monitor. The digitalized calls were analyzed with Sound Forge 6.0 Demo (Sonic Foundry 2003), AVISOFT SASLab Light for Windows 3.74 (Avisoft Bioacustics 1999) using the software settings as follows: FFT=256; Frame=100; filter flap top and contrast char=5. Sonogram structure, as well as, the oscillogram and power spectrum of the *C. yacare* calls were statistically described and quantitatively compared intra-specifically. The comparisons with calls from other crocodilian species were qualitatively made based on literature. All records are digitally preserved in the Laboratory of Bioacoustics, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Brazil.

Because adult female caimans tend to remain near the nests, we conducted searches during daytime (07:00hr-12:00hr, and 15:00hr-17:30hr, avoiding high temperatures in the following hours after noon) by locating the nests through the dense bromeliad vegetation (*Bromelia balansae*), which surrounds the freshwater ponds locally known as "baías" (*i.e.* "bays"). The mere approaching was enough to stimulate the aggressive behavior and vocalization by nest-guarding females; otherwise, they usually vocalized after our attempts to capturing them with a snare pole.

During the second visit to the study area, searchlights were used to locate young caimans on the flooded grassland along the bay shores, one hour after the sunset (from 19:00hr to 00:00hr). Young caimans were captured along eight bays in the study area (Fig. 1), had their vocalizations recorded and, then, they were immediately released. Each bay was visited twice (total=16 visits), and the capturing procedure was conducted overnight. Some of the collected juvenile caimans were released on the following day (08:00hr-11:00hr) at the same capture site. These individuals, after few minutes to acclimate to the grassland around the bays, were then recaptured. This procedure was used to simulate a predator attack at daylight, without the interference of the dazzling searchlights. Both vocalizations emitted during the nocturnal and diurnal captures were recorded and analyzed.

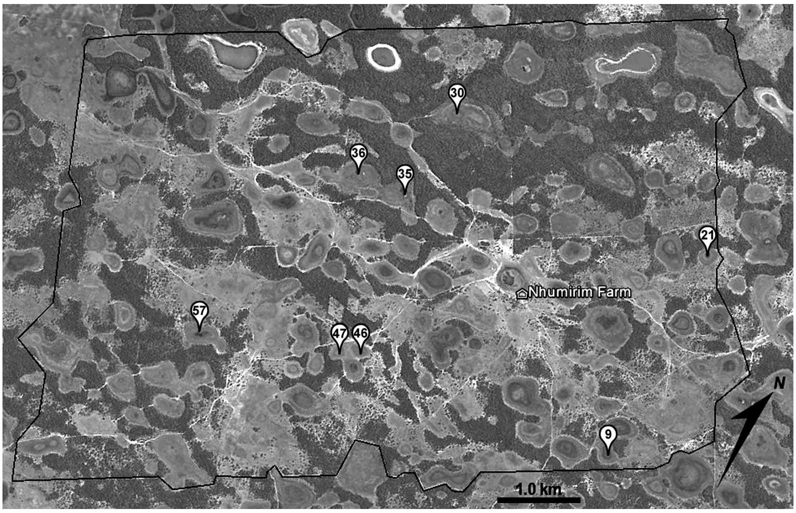

Fig. 1. Satellite image of Nhumirim Farm at April 22, 2010; estimated eye altitude: 6.77km (Google Inc. 2011). The bays where the data were collected are indicated by numbers in white landmarks. Dark grey areas correspond to the xeric and semideciduous vegetation, while the light grey parts correspond to seasonally flooded areas.

Due to the practical impossibility of determining which vocalization belonged to each individual, the calls were separated according the bays where the individuals were captured reckoning the photoperiod/stimuli type. Thus, the analyses considered groups of calls as representative to the similar aged pods of each bay.

During the field activities, we reproduced playbacks of recorded distress calls nearby the bays during the nighttime in the presence of adult caimans. The aim was to stimulate their response to calls of young caimans from different pods and bays. Random vocalizations of young caimans from pods recorded on different bays were replayed by the Uher 4 000 Report-L during 5min and, approximately, 3m from the margin of the bays where adult caimans could be seeing. On other occasions, researchers also performed rough imitations of distress calls to provoke behavioral responses from the adult caimans. These attempts, however, lacked of formal methodology (*i.e.* duration time, distance, and the individual performing the imitation), but aimed to test whether adult caimans would respond to these fake distress calls.

The structure of the vocalizations were then quantified and statistically described and compared. The different samples were tested for distribution Normality, kurtosis, skewness and homoscedasticity (Shapiro-Wilk's and Levene's Tests respectively). Non-parametric univariate tests (Kruskal-Wallis and Mann-Whitney tests) were used to direct comparisons between groups of calls.

The calls referent to individuals of different bays were also compared by Canonical Discriminant Analysis (CDA) in order to characterize the acoustic space of each group and to establish the Mahalanobis multivariate distance between them. Canonical discriminant function analysis was performed using the pods as *a priori* groups. The discriminant function analysis addresses the question of how well two or more groups of individuals could be separated through measurements taken from these individuals in several variables (Manly 1994). The individuals with more multivariate similarities (according to the measurements) are grouped and the distance of each individual to the centroid of the groups indicates the degree of similarity among them. The Mahalanobis distances of individuals to each group centroid are calculated and, then, each individual can be allocated to the group that it is closely related. The individuals may or may not be included in the *a priori* group that it initially belongs: the degree of correct allocation of individuals to the *a priori* groups is an indication of how well the groups can be separated according the variables used (Manly 1994). The significance of the overall discrimination is given by the Wilks' Lambda. The *post-hoc* test of significance used to assess the statistical multivariate difference between groups was based on the Mahalanobis distance between the centroid of each group (Manly 1994). The samples had their normality and homocedasticity tested, as well as the skewness and kurtosis of distributions. The geographic distances between the bays where the calls were collected were established through the Google Earth 6.1 (Google Inc. 2011). The existence of a correlation between the two distance matrices (Mahalanobis and geographic) was tested by Mantel Test. The statistical packages used were Statistica 8.0 (StatSoft 2009) and BioEstat 5.0 (Ayres *et al.* 2007).

RESULTS

Vocalization and behavior of adult Paraguayan caiman females: We found 18 caiman nests, but adult *C. yacare* females were present only in 11 of them. The adult females were camouflaged in bromeliads and about 2m from the nest. The caiman females were recorded demonstrating the aggressive vocal display reported for other crocodilian species during nest guarding. Two females displayed the full nest defense behavior; that is, after the aggressive vocalization, they chased the "intruders" with short rapid movements causing a loud disturbance in the surrounding vegetation.

Aggressive vocalizations emitted by *C. yacare* adult females start with a deep inhalation (causing an apparent increasing in the caiman body), followed by air exhalation and a prolonged growl associated with an acute hiss with an average duration of 400ms (SD=18, n=11). The vocalization analysis indicated that this hiss seems like a white noise without a melodic structure (*i.e.,* no evident harmonic formation; Fig. 2). In 57.1% of these calls, pulsed sounds of low frequency accompany the hiss. Despite the variant structure of this kind of vocalization, three marked patterns were recognized (Fig. 3) in different individual records. These calls may include the

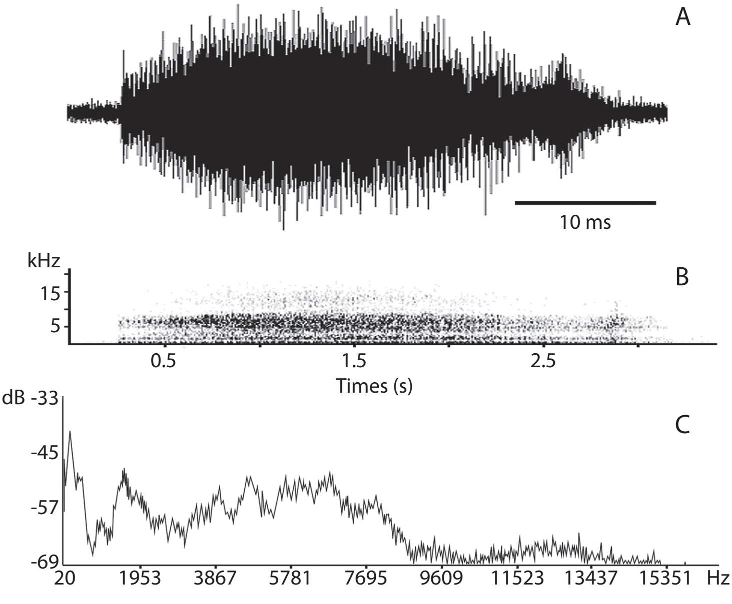

Fig. 2. Analysis of the adult Paraguayan caiman female aggressive call during the nest guarding. The call structure is presented through: (A) oscillogram (waveform), (B) audio spectrogram, and (C) frequency spectrum.

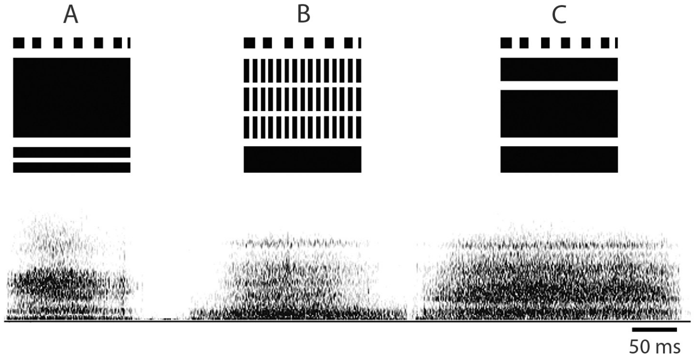

Fig. 3. Three different patterns (A, B and C) of adult Paraguayan caiman female aggressive call during the nest guarding.

presence of one or two distinct baselines (average minimum and maximum-AMM: 28.4Hz to 2151.1Hz) accompanied by a higher broad band that could be slightly separated in some calls (AMM: 2957.1Hz to 8842.9Hz). Above these bands, a high frequency continuous, or intermittent, band was found ranging to an average maximum of 16457.1Hz. The average dominant frequency was 279.4Hz at the first peak and 2312.3Hz at the second peak.

When playbacks of the distress calls were played, the adult caimans responded with approximations toward the source of the calls. This behavior could be observed in eight out of 10 times when this experiment was performed. These adult caimans rushed warily toward the source of the playbacks regardless the fact of the distress calls belonged to pods of different bays of origin. Responses to ours imitations of the distress call were also observed. Nevertheless, none adult caiman displayed the full aggressive behavior usually described for these situations, limiting their response to swim toward the source of the calls, but they never coming closer than 4m.

Vocalization and behavior of young Paraguayan caimans: A total of 196 calls were recorded from several individuals from different pods, all of them with less than two months old. We observed that when a young *C. yacare* is disturbed, it runs/swims away vocalizing, while the other members of the pod follows the same behavior despite not have been directly stimulated.

The distress call of young caimans, according the sonographic analysis, consists of short notes with defined harmonic structure (Fig. 4). Sonograms revealed the formation of up to 12 harmonics, which swept downward with declining modulation. In some cases, an initial short and quick upsweep modulation was observed. The average duration of the total vocalizations of young *C. yacare* of less than two months old was 141.63ms (SD=38.50). The coefficient of variation is relatively high, 27.18%, denoting the large individual variation of duration of juvenile distress calls (Fig. 5). The upsweep modulation was found in 67.35% of the calls and, in such cases, it corresponds to 15.46% of total duration of the call (SD=8.87). The average dominant harmonic frequency was 1 456.01Hz (SD=279.04) and in 84.18% of the calls, the dominant harmonic was the third; in 13.78%, it was the second, and only in 2.04%, it was the forth. The average minimum and maximum frequencies of the fundamental harmonic were, respectively, 137.95Hz and 620.60Hz.

Comparing the total vocalizations collected by night with searchlights and manipulation of the individuals (n=154), and by day with simulated attempts of capture (n=42), we found differences in the calls' structure in six out of

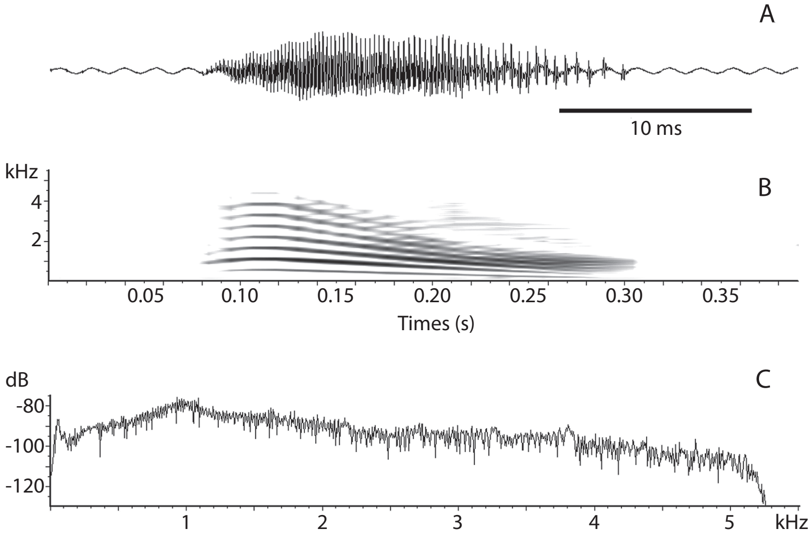

Fig. 4. Analysis of the juvenile Paraguayan caiman distress call. The call structure is presented through: (A) oscillogram (waveform), (B) audio spectrogram, and (C) frequency spectrum.

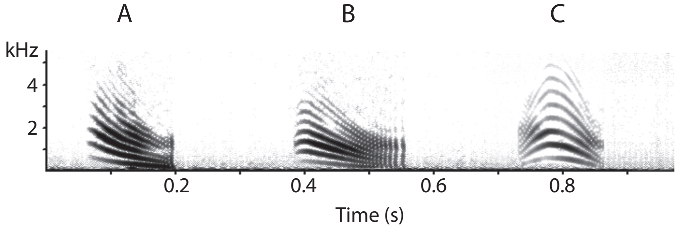

Fig. 5. Three different patterns of young Paraguayan caiman distress call (A, B, and C) recorded in similar experimental conditions. Note the circumflex pattern observed on C as described by Britton (2001) to *Crocodylus niloticus* and *Crocodylus johnsoni*.

nine parameters analyzed. The vocalizations collected during the night captures were longer (average total duration=150.49ms, SD=37.00) than the calls during the day release-and-recapture procedure (total duration=109.34ms, SD=24.00), Mann-Whitney's U=1 035.0, $p<0.001$. However, the ratio between the total duration and the duration of the ascendant modulation (when it was present) was higher in the daytime collected calls (21.30, SD=12.62%), than in the night-time ones (13.10, SD=5.26 U=982.5, $p<0.001$). On the other hand, the dominant frequency of the calls showed no variation between the different photoperiods and styles of capture ($p>0.95$). Despite the significant quantitative differences found in the maximum frequency of the fundamental harmonic (U=1 914.0, $p<0.001$), maximum and minimum frequencies of the second harmonic (U=2 165.0, $p<0.01$ and U=2 585.0, $p<0.05$ respectively), and the maximum frequency of the third harmonic (U=2 398.5, $p<0.02$), such differences are negligible at the biological point of view.

The structure of the calls of the young caimans from three out of eight bays (Bays 21, 46, and 47) where vocalizations were collected was compared according to the hour and style of stimuli. The total duration of the calls collected by night was longer than the calls of the same groups of juveniles during the day experiment (Bay 21, $n_{[night]}=78$, $n_{[day]}=8$, U=23.5, p<0.001; Bay 46, $n_{[night]}=22$, $n_{[day]}=9$, U=2.5, p<0.001; and Bay 47, $n_{[night]}=13$, $n_{[day]}=17$, U=0.0, p<0.001).

Following the trend observed on the pooled-within analysis, the ratio the duration of the upsweep modulation (when it was present in the calls) and total duration of the call, was significantly higher in the nocturnal experiment than in the diurnal experiment, in the bays 46 (U=0.0, p<0.001) and 47 (U=6.5, p<0.001). No significant difference was observed in the ratio of the upsweep modulation by the total duration of the calls of the young caimans of the Bay 21 (U=70.0, p>0.17) regarding the time of the day and style of sampling.

A slight difference between the average values of the dominant harmonic frequency of the distress calls was observed in the Bay 47, regarding the time of the day (nocturnal=1 505.39Hz e diurnal=1 251.18Hz, U=46.5, p<0.01). No other difference was detected in the call samples along the other bays.

Since significant differences were observed between the distress call structure according the time of the day and sampling styles, this fact was taken into account in the comparisons between the juveniles' vocalizations from different bays. The young caiman calls of the five best-sampled bays (Bays 9, 21, 35, 46 and 47) were compared regarding their total duration and dominant harmonic frequency. These parameters were used to perform the CDA in order to differentiate the calls according their bay of origin and to obtain the Mahalanobis distances between the acoustic spaces. The factor structure of the canonical roots, as well as, the eigenvalues of the CDA, of the both nocturnal and diurnal experiments, were presented in tables 1 and 2. The results of the squared Mahalanobis distances matrices, as well as, the matrices of geographic distances between the bays, were summarized in tables 3 and 4.

We observed significant differences in the vocalization structure according to bay of origin in both experiments. It means that geographic differences exist among the calls recorded during the young caimans capture by night, while they were stunned by the searchlights, as well as in the calls recorded during the daytime releasing of the young caimans when (after few moments) they were recaptured (Wilks' Lambda=0.54, F=12.96, d.f.=8, 290, p<0.001 and Wilks' Lambda=0.19, F=15.99, d.f.=6, 74, p<0.001, respectively). Nevertheless, the Mantel Test of correlation between the matrix of Mahalanobis distance of the calls structure and the matrix of geographic distance between the bays of origin indicated no significant correlation in both experiments (nocturnal: Mantel's Coefficient of Correlation=0.01, d.f.=8, p>0.96, and diurnal: Mantel's Coefficient of Correlation=0.65, d.f.=4, p>0.16).

TABLE1

Factor structure, variable loadings and eingenvalues of Canonical Discriminant Analysis of the acoustic variables of young caimans during the nocturnal experiment

Variables	Root 1	Root 2
Total Duration	-0.9957	-0.0928
Dominant Harmonic Frequency	0.1491	-0.9888
Eigenvalues	0.63258	0.128990
Cummulative Expalined Variation	83.03%	100.00%

TABLE 2

Factor structure, variable loadings and eingenvalues of Canonical Discriminant Analysis of the acoustic variables of young caimans during the diurnal experiment

Variables	Root 1	Root 2
Total Duration	-0.9943	-0.1064
Dominant Harmonic Frequency	0.0035	-0.9999
Eigenvalues	2.70649	0.422323
Cummulative Expalined Variation	86.50%	100.00%

DISCUSION

Aggressive response of adult *C. yacare* females compared to other Alligatoridae: The nest guarding behavior was present in 61.1% of the Paraguayan caiman nests in this study. Ayarzagüena (1983), based on 30 observations in Venezuelan llanos, reported that

TABLE 3
Matrixes of geographic and Squared Mahalanobis distances between pods during the diurnal experiment

(A)	Bay number	9	21	35	46
	21	3.16 (p<0.001)*	-	-	-
	35	3.07 (p<0.001)*	6.90 (p<0.001)*	-	-
	46	2.14 (p<0.001)*	0.18 (p>0.22) ns	4.86 (p<0.001)*	-
	47	1.14 (p<0.01)*	0.95 (p<0.01)*	2.82 (p<0.01)*	0.31 (p>0.29) ns
(B)	Bay number	9	21	35	46
	21	2.72	-	-	-
	35	4.06	3.77	-	-
	46	3.29	4.38	1.97	-
	47	3.56	4.66	2.07	0.28

Matrix of Squared Mahalanobis distances between the acoustic spaces of distress calls of pods according the bays (A). Distance matrix in kilometers between the bays where the distress calls of the respective pods were recorded (B). Distances between the same bays were omitted.
* indicates that p-values of the distances are significant, ns means non-significant.

TABLE 4
Matrixes of geographic and Squared Mahalanobis distances between pods during the nocturnal experiment

(A)	Bay number	21	46	47
	46	2.82 (p<0.01)*	-	-
	47	8.63 (p<0.001)*	2.00 (p<0.01)*	-
	57	24.24 (p<0.001)*	10.80 (p<0.001)*	7.21 (p<0.001)*
(B)	Bay number	21	46	47
	46	4.38	-	-
	47	4.66	0.28	-
	57	6.20	1.92	1.68

Matrix of Squared Mahalanobis distances between the acoustic spaces of distress calls of pods according the bays (A). Distance matrix in kilometers between the bays where the distress calls of the respective pods were recorded (B). Distances between the same bays were omitted.
* indicates that p-values of the distances are significant.

70% of *C. crocodilus* females presented the guarding nests behavior after laying. However, Crawshaw & Schaller (1980) pointed out that *C. yacare* females are rarely present at a nest in daytime, but often can be seen in adjacent water bodies. Therefore, it remains unclear if the nest guarding in *C. yacare* females is significantly different from the *C. crocodilus*. The full aggressive behavior, characterized by the initial intimidating hiss/growl followed by rapid movements towards the researchers, exhibited by two *C. yacare* was similar to that reported for *C. crocodilus* against natural egg predators by Ayarzagüena (1983).

The aggressive vocalizations emitted by *Alligator mississipiensis* females in similar circumstances of nest defense, described by Garrick *et al*. (1978) as a simple hiss, showed frequencies under 1kHz between 1-3s of duration. Thus, nest guarding vocalization of the adult *C. yacare* females observed was longer, with an average duration of 4.0s, and seems to be more complex than that emitted by *A. mississipiensis*, showing three different structural patterns.

Distress call of young *C. yacare* compared to other crocodilians: Vocalizations of young *C. yacare* (less than two months old) recorded in Pantanal of Nhecolândia presented the acoustic structure consistent with Vergne's *et al.* (2009) description of the distress call of young crocodilians. Qualitative comparisons between sonograms of distress calls of *C. yacare*, *A. mississipiensis*, *Crocodylus acutus*, *Melanosuchus niger*, and *C. fuscus* (treated by Campbell (1973) as *C. crocodilus* in Panama) revealed differences among them. We found differences on harmonic number, duration of call, and presence or absence of upsweep modulations at the beginning of the note. These comparisons were based on Campbell's (1973) descriptions, although in his paper, he made no references to individual variations in the distress call of those other crocodilian species. Moreover, Campbell (1973) presented vocalizations of juvenile individuals of different size and age, thus the comparisons made here could be biased by intrinsic ontogenetic vocal variation. *A. mississipiensis* shows a simpler acoustic structure; the fundamental begins at about 0.6kHz and sweeps downward to about 0.3kHz in approximately 0.1s. Two main harmonics spring clearly at 0.8kHz and 1.2kHz. The remaining crocodilians examined by Campbell (1973) shows a more complex acoustic structure in their calls. In *C. fuscus* the call structure has the fundamental beginning at approximately 0.7kHz and sweeps downward to about 0.2kHz in 0.1s, with several harmonics present. *C. acutus* call structure has a fundamental beginning at 0.6-0.5kHz and sweeping down to 0.3-0.2kHz; several weak harmonics are presents in the juveniles but the harmonic present in the hatchlings are stronger (Campbell 1973). Despite some structural similarities, the distress call of *M. niger* is shorter than that of *C. yacare* and the lower frequency lies at 0.2kHz.

Nevertheless, our results are quite congruent with Vergne *et al.* (2007) results for young *Crocodylus niloticus* that present a marked individual variation. However, the average total duration of *C. niloticus* juvenile distress calls is longer (206.00ms±39ms) than that of *C. yacare* (146.63ms±38.5ms). The distress call structure of young *C. yacare* ranges from the pronounced frequency modulation with simple downsweep slopes, to complex initial upsweep modulations followed by the downsweep modulation described by Britton (2001) as "circumflex" shape. The circumflex shaped calls are reported as featured for *C. niloticus* and *Crocodylus johnsoni* (Britton 2001, Vergne *et al.* 2009). Vergne *et al.* (2009) pointed out that there is a high change in the individual acoustic structure of the calls along the days following hatching. Among other Caimaninae, the distress call of *C. yacare* seems to be longer than that of *M. niger* (100ms±20ms) as indicated by Vergne *et al.* (2011).

Intraspecific vocal variations among juvenile Paraguayan caimans: Our quantitative analysis also indicates that a high variability in the structure of the distress call exists among different pods of young Paraguayan caiman. We, however, regarded the differences in the call structure during the nocturnal and diurnal experiments to an effect of the juveniles' manipulation during the capture, rather than a biological circadian variation. On the other hand, the variation in the call structure observed in vocalizations of pods of different bays of origin is evident and statistically significant, even to pods separated by few kilometers in a relatively small area of 4 800Ha.

Nevertheless, the degree of similarity or difference in the call structure between pods, measured by the squared Mahalanobis distance (and associated p-value), is not correlated to the geographic distance between the bays where the calls where collected. Thus, if the distance between pods is not contributing to distress call heterogeneity, other factors must be.

During nocturnal activities, adult caimans could be observed swimming nearby the source of the distress calls. We observed adult individuals of *C. yacare* (possibly the parent female of those pods) reacting to calls of the juveniles, usually by coming closer to the source of the calls. Nevertheless, we observed adults displaying this same behavior, when recorded distress calls of other pods were played back, and even when rough imitations of the young caimans' calls were made by us. A similar unspecific parental response to juveniles' calls was observed by Campbell (1973) in adult *A. mississipiensis,* which reacted to distress calls from other species. The adult caimans seem to display the parental care to anything similar to the young caimans' distress call. However, the typical aggressive behavior of the adult caimans against predators of juveniles described in the literature (Ayarzagüena 1983, Romero 1983, Allsteadt & Vaughan 1988) was not observed in our field work. Only one adult approached about 4m from us and then, swam away without attacking.

Distress call of young *C. yacare*: does the variability favored by natural selection?: During our field observations, in the most of the cases, the parental protection in *C. yacare* is granted even to high heterogeneous calls of juveniles in distress situations. Thus, based on these field experiments and in the high variability of the distress call structure assessed, we hypothesize that adult caiman females present low specificity in the recognition of the juvenile distress call. Consequently, this might reduce the stabilizing selection of this character. According to Passek & Gillingham (1999), young alligators usually get assembled in pods regardless if they are kin or not. No preferential signaling between kin juveniles seems to be present between alligators. If one assumes that the same could be true for the Paraguayan caiman, then this could contribute to increase the variance of the distress call acoustic structure within the pods. The adaptative advantage would be the protection of any juvenile despite their origin, since the adult caimans are usually attracted to anything similar to a distress call.

On the other hand, the answer to why the geographic distance was not correlated to the statistical distance between the acoustic spaces in the CDA lies in the complexity of the Pantanal of Nhecolândia landscape. The geographical distance may be not a natural barrier by itself, however, nearby bays may be more isolated due to dry soil elevations and dense vegetation than the more distant ones. Therefore, epigenetic morphofunctional variations in the vocal apparatus of the young *C. yacare*, the absence of social connection between pods of different bays, and the low negative selection related to the adults response, would act as synergic factors increasing the variability in the distress call s of the juvenile Paraguayan caimans.

ACKNOWLEDGMENTS

We are indebt with the curator of the Laboratory of Bioacustics of Universidade Federal do Rio de Janeiro, Luiz Gonzaga for the support with the recording equipment and digitalizing the records, as well as with Sergio Carvalho-e-Silva, chairman of the Laboratory of Herpetology of Universidade Federal do Rio de Janeiro, and Eugênio Izecksohn, from Universidade Federal Rural do Rio de Janeiro, for their help in discussing the data. We also thank the administrators of the Nhumirim Farm for granted the access to the area. We are grateful to Christopher Vaughan and Mahmood Sasa for their kindly review of the first versions of the manuscript, as well as Bryan Jennings for reviewing the last version. This study had financial support by CPEG Grant Program – Universidade Federal do Rio de Janeiro, and by BioVasc– Universidade do Estado do Rio de Janeiro, Brazil.

RESUMEN

Poco se conoce sobre la estructura vocal del *Caiman yacare* del Pantanal brasileño. Llamadas agresivas de hembras adultas que cuidaban de los nidos fueron registradas durante enero y febrero y llamadas de socorro de caimanes jóvenes, en abril de 1992. Hembras adultas de *C. yacare* presentaron una vocalización agresiva más larga y compleja que en otras especies más grandes de Alligatoridae.

Las vocalizaciones de los jóvenes caimanes también presentaron diferencias interespecíficas con otros cocodrilos y variaciones intraespecíficas entre grupos separados por pocos kilómetros. Se utilizó la Prueba de Mantel para comparar las distancias de Mahalanobis entre la estructura de las vocalizaciones de los jóvenes de acuerdo con sus grupos y las distancias geográficas donde ellos estaban. La distancia geográfica en sí no explica las diferencias en las vocalizaciones de jóvenes de diferentes grupos. Hembras adultas de *C. yacare* han respondido a grabaciones de llamadas de caimanes de grupos de otras regiones, así como a imitaciones de llamada de socorro. Se postula que las variaciones en las llamadas de socorro pueden estar asociadas con una baja especificidad en el reconocimiento de sonido por caimanes adultos que han respondido de la misma forma protectora a las más heterogéneas expresiones de peligro de los jóvenes.

Palabras clave: yacaré del Pantanal, Caimaninae, llamada de socorro, vocalización, cuidado parental, sonogramas, métodos estadísticos multivariantes.

REFERENCES

Alho, C.J.R., T.E. Lacher & H.C. Goncalves. 1988. Environmental degradation in the Pantanal ecosystem in Brazil, the world largest wetland is being threatened by human activities. Bioscience 38: 164-171.

Alho, C.J.R. 2008. Biodiversity of the Pantanal: Response to seasonal flooding regime and to environmental degradation. Braz. J. Biol. 68: 957-966.

Allsteadt, J. & C. Vaughan. 1988. Distress calls of caiman, *Caiman crocodilus fuscus*, in northern Costa Rica. Rev. Biol. Trop. 36: 567-568.

Avisoft Bioacustics. 1999. Avisoft Saslab light for windows, software version 3.74. Berlin, Germany.

Ayarzagüena, S.J. 1983. Ecología del caiman anteojos o baba (*Caiman crocodilus* L.), en los llanos de Apure (Venezuela). Doñana Acta Vert. 10: 75-102.

Ayres, M., M. Ayres Jr., D.L. Ayres & A.S.S. dos Santos. 2007. Biostat, version 5.0. Belém, Pará, Brazil.

Benko, T.P. & M. Perc. 2009. Nonlinearities in mating sounds of American crocodiles. Biosystems 97: 154-159.

Bond, A.B. & J. Diamond. 2005. Geographic and ontogenetic variation in the contact calls of the kea *Nestor notabilis*. Behaviour 142: 1-20.

Brazaitis, P. 1973. Identification of living crocodilians. Zoologica 59: 59-101.

Brazaitis, P., G.H. Rebelo & C. Yamashita. 1998. Distribution of *Caiman crocodilus crocodilus* and *Caiman yacare* populations in Brazil. Amphibia-Reptilia 19: 193-201.

Britton, A.R.C. 2001. Review and classification of call types of juvenile crocodilians and factors affecting distress calls. *In* G.C. Grigg, F. Seebacher & C.E. Franklin (eds.). Crocodilian biology and evolution. Chipping Norton, New South Wales, Australia.

Brochu, C.A. 1999. Phylogenetics, taxonomy, and historical biogeography of Alligatoroidea. J. Verteb. Paleontol. 19: 9-100.

Busack, S.D. & S. Pandya. 2001. Geographic variation in *Caiman crocodilus* and *Caiman yacare* (Crocodylia : Alligatoridae): Systematic and legal implications. Herpetologica 57: 294-312.

Campbell, H.W. 1973. Observations on acoustic behavior of crocodilians. Zoologica spring: 1-11.

Campos, Z., A.Q. Llobet, C.I. Piña & W.E. Magnusson. 2010. Yacare caiman (*Caiman yacare*). *In* S.C. Manolis & C. Stevenson (eds.). Crocodiles: Status survey and conservation action plan. Crocodile Specialist Group, Darwin, Australia.

Cintra, R. 1988. Nesting ecology of the Paraguayan caiman (*Caiman yacare*) in the Brazilian Pantanal. J. Herpetol. 22: 219-222.

Crawshaw, P.G. & G.B. Schaller. 1980. Nesting ecology of Paraguayan caiman (*Caiman yacare*) in Brazil. Pap. Avulsos Zool. 33: 238-292.

Escobedo-Galvan, A.H., F.G. Cupul-Magana & J.A. Velasco. 2011. Misconceptions about the taxonomy and distribution of *Caiman crocodilus chiapasius* and *C. crocodilus fuscus* (Reptilia: Crocodylia: Alligatoridae). Zootaxa 3015: 66-68.

Fitch, W.T. 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. J. Acoust. Soc. Am. 101: 1213-1222.

Fitch, W.T. 2000. Skull dimensions in relation to body size in nonhuman mammals: The causal bases for acoustic allometry. Zoology 103: 40-58.

Garrick, L.D., J.W. Lang & H.A. Herzog. 1978. Social signs of adult American alligators. B. Am. Mus. Nat. Hist. 160: 154-192.

Google Inc. 2011. Google earth, software version 6.1. Mountain View, California, USA.

Gorzula, S. 1985. Are caimans always in distress? Biotropica 17: 343-344.

Hrbek, T., W.R. Vasconcelos, G. Rebelo & I.P. Farias. 2008. Phylogenetic relationships of South American alligatorids and the caiman of Madeira River. J. Exp. Zool. Part A 309A: 588-599.

Hunt, R.H. & M.E. Watanabe. 1982. Observations on maternal-behavior of the American alligator, *Alligator mississippiensis*. J. Herpetol. 16: 235-239.

King, F.W. & R.L. Burke. 1989. Crocodilian, tuatara and turtles species of the world. A taxonomic and geographic reference. Association of Systematics Collections, Washington, DC, USA.

Magnusson, W.E. 1980. Hatching and creche formation by *Crocodylus porosus*. Copeia: 359-362.

Manly, B.F.J. 1994. Multivariate Statistical Methods: a Primer. Chapman & Hall, London, England.

Martin, S. 2008. Global diversity of crocodiles (Crocodylia, reptilia) in freshwater. Hydrobiologia 595: 587-591.

Oaks, J.R. 2011. A time-calibrated species tree of Crocodylia reveals a recent radiation of the true crocodiles. Evolution 65: 3285-3297.

Passek, K.M. & J.C. Gillingham. 1999. Absence of kin discrimination in hatchling American alligators, *Alligator mississippiensis*. Copeia: 831-835.

Riede, T. & I.R. Titze. 2008. Vocal fold elasticity of the Rocky Mountain elk (*Cervus elaphus nelsoni*)-producing high fundamental frequency vocalization with a very long vocal fold. J. Exp. Biol. 211: 2144-2154.

Riede, T., I.T. Tokuda & C.G. Farmer. 2011. Subglottal pressure and fundamental frequency control in contact calls of juvenile *Alligator mississippiensis*. J. Exp. Biol. 214: 3082-3095.

Romero, G.A. 1983. Distress call saves a *Caiman c. crocodilus* hatchling in the Venezuelan Llanos. Biotropica 15: 71-71.

Sonic Foundry. 2003. Sound Forge demo, software version 6.0. Madison, Wisconsin, USA.

Stanton, M.A. 1978. “Distress calls” of crocodilians-whom do they benefit? Am. Nat. 112: 327-332.

StatSoft. 2009. Statistica (data analysis software system), version 8. Tulsa, Oklahoma, USA.

Velasco, A. & S.J. Ayarzagüena. 2010. Spectacled *Caiman caiman crocodilus*. *In* S.C. Manolis & C. Stevenson (eds.). Crocodiles: Status survey and conservation action plan. Crocodile Specialist Group, Darwin, Northern Territory, Australia.

Vergne, A.L., A. Avril, S. Martin & N. Mathevon. 2007. Parent-offspring communication in the Nile crocodile *Crocodylus niloticus*: Do newborns’ calls show an individual signature? Naturwissenschaften 94: 49-54.

Vergne, A.L. & N. Mathevon. 2008. Crocodile egg sounds signal hatching time. Curr. Biol. 18: R513-R514.

Vergne, A.L., M.B. Pritz & N. Mathevon. 2009. Acoustic communication in crocodilians: From behaviour to brain. Biol. Rev. 84: 391-411.

Vergne, A.L., T. Aubin, P. Taylor & N. Mathevon. 2011. Acoustic signals of baby black caimans. Zoology 114: 313-320.

Vliet, K.A. 1989. Social displays of the American alligator (*Alligator mississippiensis*). Am. Zool. 29: 1019-1031.

Wang, X.Y., D. Wang, X.B. Wu, C.L. Wang, R.P. Wang & T.S. Xia. 2009a. Response specificity to advertisement vocalization in the Chinese alligator (*Alligator sinensis*). Ethology 115: 832-839.

Wang, X.Y., D. Wang, S. Zhang, C.L. Wang, R.P. Wang & X.B. Wu. 2009b. Why do Chinese alligators (*Alligator sinensis*) form bellowing choruses: A playback approach. J. Acoust. Soc. Am. 126: 2082-2087.

Wever, E.G. 1971. Hearing in the Crocodylia. Proc. Natl. Acad. Sci. USA 68: 1498-1500.