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Vocal repertoire of the social giant otter

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According to the "social intelligence hypothesis," species with complex social interactions have more sophisticated communication systems. Giant otters (*Pteronura brasiliensis*) live in groups with complex social interactions. It is likely that the vocal communication of giant otters is more sophisticated than previous studies suggest. The objectives of the current study were to describe the airborne vocal repertoire of giant otters in the Pantanal area of Brazil, to analyze call types within different behavioral contexts, and to correlate vocal complexity with level of sociability of mustelids to verify whether or not the result supports the social intelligence hypothesis. The behavior of nine giant otters groups was observed. Vocalizations recorded were acoustically and statistically analyzed to describe the species' repertoire. The repertoire was comprised by 15 sound types emitted in different behavioral contexts. The main behavioral contexts of each sound type were significantly associated with the acoustic variable ordination of different sound types. A strong correlation between vocal complexity and sociability was found for different species, suggesting that the communication systems observed in the family mustelidae support the social intelligence hypothesis. © 2014 Acoustical Society of America. [http://dx.doi.org/10.1121/1.4896518]

I. INTRODUCTION

Animals communicate through different kinds of signals, which presumably increases their fitness (Bradbury and Vehrencamp, 1998; Wilson, 2000). The content of signals may provide information about the status, motivation, and identity of senders and may vary according to behavioral contexts and the environment (Bradbury and Vehrencamp, 1998). Vocal signals are usually classified according to the behavioral context in which they are used, and thus, their function in communication (Bradbury and Vehrencamp, 1998). Although many mammal species present a continuous repertoire of sounds, vocal repertoire analysis usually aims to discriminate discrete sound types that are associated with different behavioral contexts, as described in a wide range of species, including otters (e.g., Schassburger, 1993; Sieber, 1984; McShane *et al.*, 1995; Wong *et al.*, 1999; Lemasson *et al.*, 2014).

Behavioral context and the motivational state of senders influence the use of different signals as well as their structure (Morton, 1977; August and Anderson, 1987). The "social intelligence hypothesis" proposes that species living in more complex social groups present a more sophisticated communication system ("large number of structurally and functionally distinct elements or a high amount of bits of information," Freeberg *et al.*, 2012), which is necessary to deal with a wider range of social interactions in different behavioral contexts. Moreover, the use of gradations and combinations of sounds may result in more complex repertoires and increase the number of messages that can be transmitted (Schassburger, 1993; Wilson, 2000). Therefore, large and graded repertoires are expected to occur with greater frequency in highly social species, compared to solitary or non-social animals (Bradbury and Vehrencamp, 1998; McComb and Semple, 2005).

Mustelid sociability has been categorized as a dichotomous system (primarily solitary versus highly gregarious) (Creel and Macdonald, 1995; Wong *et al.*, 1999) or as discrete degrees of sociality (solitary, pairs, variable groups, groups) (Johnson *et al.*, 2000). Mustelid social systems vary greatly within species and may also be correlated with ecological factors that change in space and time (Johnson *et al.*, 2000). According to the classification of sociability, as

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suggested by Johnson *et al.* (2000), giant otters (*Pteronura brasiliensis*) and small-clawed otters (*Aonyx cinerea*) show the highest degrees of sociability within mustelids. These are followed by species that form groups of variable sizes, such as Zaire clawless otters (*Aonyx congicus*), sea otters (*Enhydra lutris*), European river otters (*Lutra lutra*), spot-necked otters (*Lutra maculicollis*), North American river otters (*Lontra Canadensis*), and badgers (*Meles meles*).

Giant otters live in cohesive groups of two to 20 individuals (Duplaix, 1980; Leuchtenberger and Mourão, 2008), including a dominant breeding pair and other individuals that may or may not be genetically related (Ribas, 2012). Group members help in caring for the offspring of the dominant pair, whose reproductive period in nature is around 10 yr for females and 15 yr for males (Davenport, 2010). Subadults usually leave their natal group when they achieve sexual maturity at around 2 years of age (Duplaix, 1980). Nonetheless, there are records of subadults leaving their social groups earlier and also remaining long after reaching sexual maturity (Leuchtenberger and Mourão, 2008). Giant otter social groups are mainly diurnal and engage in almost all of their daily activities together, such as scent-marking to delineate territories, resting on the shore, foraging, playing and defending territories from intruders with aggressive behaviors and loud vocal choruses (Duplaix, 1980; Ribas and Mourão, 2004; Leuchtenberger and Mourão, 2009; Leuchtenberger *et al.*, 2014).

Although giant otters are highly social, previous studies of their airborne vocal repertoire described only nine different sound types. These sounds were associated with behavioral contexts registered during observations of free-ranging animals in the Guyanas and the Amazon Basin (Duplaix, 1980; Staib, 2005; Bezerra *et al.*, 2010), observations of captive animals originating from the Amazon and Pantanal regions (Machado, 2004), and a few spectrographic descriptions of sounds emitted in specific contexts by free-ranging animals in the Pantanal (Ribas and Mourão, 2004; Leuchtenberger and Mourão, 2009; Ribas *et al.*, 2012). Additionally, other mustelids, such as badgers (*M. meles*) and sea otters (*E. lutris*), although presenting a lower degree

of sociability (Johnson *et al.*, 2000), show larger vocal repertoires containing complex graded signal structures compared to giant otters (McShane *et al.*, 1995; Wong *et al.* 1999).

Considering the prediction of the social intelligence hypothesis (Freeberg *et al.*, 2012) and the high degree of sociability in giant otters among mustelid species (Johnson *et al.*, 2000), we hypothesized that the vocal communication system of giant otters is likely to be more sophisticated than the past studies suggest. Since the description of vocal repertoires can be highly subjective, our first aim was to quantitatively describe the airborne vocal repertoire of giant otters in the Brazilian Pantanal and second, to associate the resultant call types with different behavioral contexts, considering that sounds vary according to the social context in which they are emitted and according to the arousal of senders. We also correlated the vocal complexity of 15 mustelid species with their degree of sociability to assess whether or not the complexity of vocal communication systems observed in the family mustelidae support the social intelligence hypothesis.

II. METHODS

A. Study site

The current study was conducted in the Nhecolândia area of the Pantanal region, a large, seasonally flooded wetland covering approximately 160 000 km^2 and located at low altitude (75–200 m a.s.l), near the geographic center of South America. The Pantanal is subject to a strong annual flood pulse, which affects the home range size of giant otter groups and may cause shifts in territory boundaries and ownership (Leuchtenberger *et al.*, 2013). The Paraguay river is the main river draining the region from north to south, and most of its tributaries flow from east to west, including the Miranda and Negro rivers where the vocal recordings and behavioral observations for this study were realized (Fig. 1).

B. Data collection and classification

We monitored five giant otter groups (G1, G2, G4, G10, and G12) on a monthly basis, from September 2009 to June
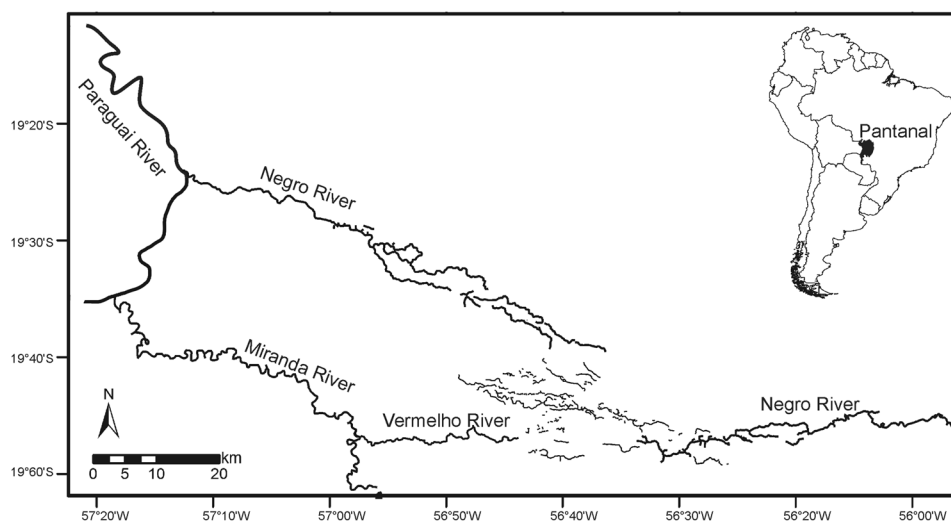

FIG. 1. Map of the study area, presenting the Miranda, Vermelho, and Negro rivers, located in the Southern Pantanal in Brazil.

2011, along a stretch of the Miranda river (19°36′S, 57°00′W) and its tributary, the Vermelho river (19°34′S; 57°01′W). Four additional groups (G17–G20) were monitored along the Negro river (19°35′S; 56°11′W) in September 2009, June and September 2010, and June 2011. Each monthly field campaign lasted from 7 to 10 days. Groups were located by conducting systematic visual surveys by boat during daylight hours (5:00–19:00 h). All data collection and field observation activities were authorized under license no. 12794/4 issued by ICMBio, the Federal Environmental Agency of Brazil, and followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes *et al*., 2011).

The locations of individuals, groups and signs of the species, such as dens and latrines, were registered with a global positioning system receptor (Garmin Etrex, Inc., Olathe, KS). Once located, a group was followed at a distance of 10–100 m, depending on the perceived shyness and general reaction of the group to observer presence, to avoid any unnecessary disturbance. Individuals were identified by the naturally occurring unique whitish markings on their throats. Whenever possible, the gender of each individual was determined and their behavior recorded during the duration of the observation period using a high-definition camcorder (Canon HF-200). Video recordings were analyzed afterward to describe behavior and identify individuals. We also identified the social status of individuals within the group based on their behaviors, such as defensive posturing and frequency of scent-marking, or by signs of lactation (for more details see Leuchtenberger and Mourão, 2009) in order to determine whether any particular sound types were attributed to dominant individuals only.

Airborne sounds were recorded with a directional microphone (Sennheiser ME-66) connected to a digital Marantaz PMD-660 recorder (AIFF format, 16-bit resolution and 44.1 kHz sampling rate). Behavioral samples of visible individuals vocalizing (senders) were filmed *ad libitum* (Altmann, 1974), and the sounds were recorded concomitantly, at a maximum distance of 50 m.

We classified the senders into three age categories according to Groenendijk *et al*. (2005): adults and subadults (>12 months), juveniles (6–12 months), and cubs (0–6 months). Since the giant otters inhabiting the study area have been monitored since 2002 (Leuchtenberger and Mourão, 2008), the exact birth month of some individuals was known. When this was not the case, the approximate age of each individual was estimated based on the behavioral features described by Groenendijk *et al*. (2005). The nine giant otter groups monitored here included a total of 43 adults (20 males, 16 females, and 7 unknown), 4 juveniles (2 male, 1 female, and 1 unknown), and 25 cubs (1 male, 1 female, and 23 unknown). During the study period, 8 cubs matured to juvenile status, and 3 juveniles became adults. Group size varied from 2 to 15 individuals, with an average of 6 individuals per group.

The behavioral contexts observed for individuals or giant otter groups during the study were classified in the following manner: (i) close contact (CC), when two or more members of the same group displayed affiliative contact; (ii)

grooming (GR), when individuals displayed self-grooming or groomed other members of the group; (iii) swimming (SW), when moving through the water; (iv) within den behavior (DE), when cubs vocalized from within the den; (v) scent-marking (SM), when individuals were scent marking and/or defecating; (vi) isolation (IS), when an individual was distant from the other members of the group and started to call looking around or toward the den; (vii) begging (BE), when an individual solicited a prey item from another individual; (viii), warning/defense (WD), when an individual caught a fish and/or was eating, and it vocalized to keep another individual away; (ix) inquiry (IN), when individuals investigated something new in their environment, sometimes adopting a periscoping posture; (x) alarmed (AL), when an individual was startled and its behavior generated attention or led other members of the group to escape; (xi) intraspecific agonistic encounter (IA), when an individual or the group engaged in conflict (physical or vocal) with a conspecific intruder; and (xii) interspecific encounter (IE), when an individual or the group faced a caiman (*Caiman crocodilus yacare*). Note that caimans may represent a threat to giant otter cubs (Duplaix, 1980), but are also a food resource for adults (Ribas *et al*., 2012).

When the whole group was involved in the same behavioral context and emitting similar sounds in a chorus (e.g., during agonistic encounters), the emission rate for the whole group was estimated as the number of sounds emitted by all group members combined during each sampling period. The average emission rate per individual was subsequently divided by the number of individuals observed vocalizing during the recording period. The monitoring interval was counted from the beginning of the visual detection of a group or individual at a maximum distance of 50 m, until the end of observations, when the subjects were lost from sight. The monitoring interval restarted when the same or another individual or group (with the same composition of individuals) was re-located during the same day. The emission rate of sounds given exclusively by a particular age category was calculated based on the time that an individual of a certain age was present during the sampling period. To determine emission rates, we only considered sounds recorded from six of the groups monitored (G1, G2, G10, G17, G18, and G20), because the other three groups (G4, G12, and G19) were very shy, which might have compromised our ability to approach without disturbing their normal behavior. We did not estimate the emission rates of individuals that reacted to observer presence by drastically changing their behavior, such as running away or inspecting the observer. Nonetheless, no new call types were observed during these particular situations.

C. Acoustical analyses

Acoustic analyses were performed using Raven Pro 1.4 (Cornell Lab of Ornithology), applying the following settings for spectrograms and power spectra: Hanning window; FFT size = 1024 and 50% overlap. Sound parameters were measured from spectrograms, oscillograms, and power spectra (Fig. 2) and used to describe and/or compare
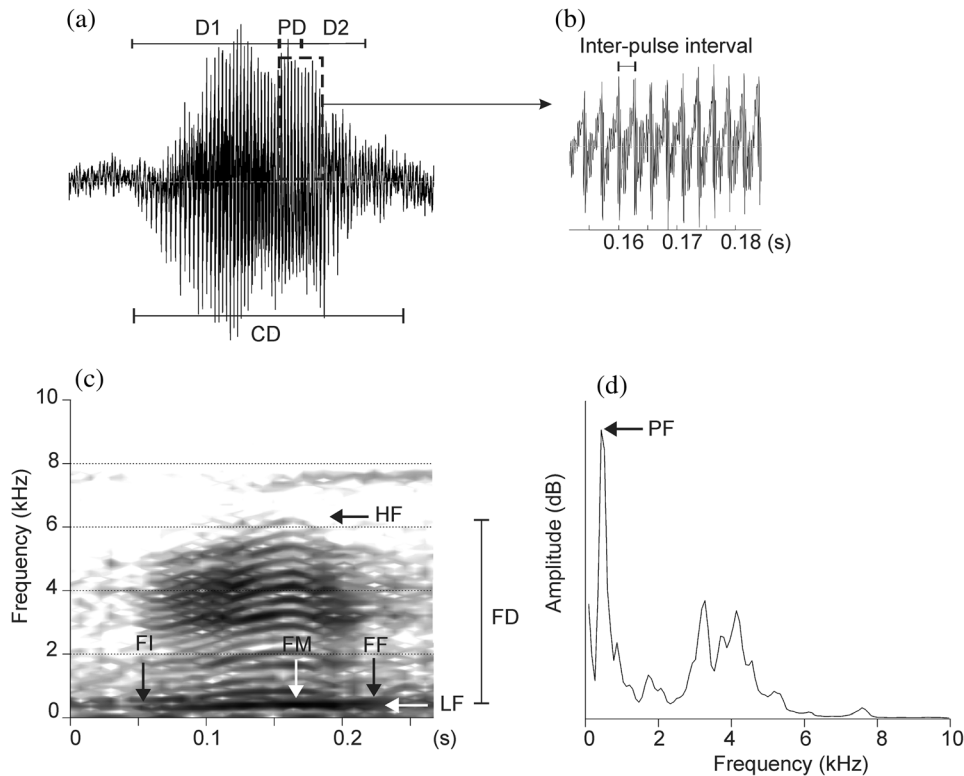
FIG. 2. Measurements of acoustic parameters of a giant-otter coo-hum call: (a) Oscillogram used to measure the total call duration (CD); the duration (D1) from the start of the vocalization to the highest value of fundamental frequency (F0) or peak frequency (PF); the duration (D2) from the highest frequency of F0 or PF to the end of the vocalization; and the plateau duration (PD), when the frequency of F0 or PF did not vary. (b) Zoom view of a stretch of the oscillogram showing the measurement of the inter-pulse interval used to estimate the number of pulses of the sound. (c) Spectrogram (window size 512) used to measure the lowest frequency (LF) of the sound; the highest frequency (HF) of the sound; the difference (FD) between HF and LF; the initial frequency (FI) of F0 or PF of the sound; final frequency (FF) of F0 or PF; and the maximum frequency (FM) of the F0 or PF. (d) Power spectrum used to measure of the PF of the selection.

vocalizations. The call parameters measured include: (CD) call duration, (LF) lowest frequency of the sound, (HF) highest frequency of the sound, (PF) peak frequency of the entire sound, (Q3) 3rd quartile frequency, this value is computed automatically by the software and represents the frequency that divides the selection into two frequency intervals containing 75% and 25% of the energy in the selection, (PU) number of pulses (temporal units that repeat rhythmically) of the sound, (FI) initial frequency of F0 (for harmonic sounds) or of the peak frequency (for non-harmonic sounds), (FM) maximum frequency of F0 or PF, (FF) final frequency of F0 or PF, (FD) difference between the highest and the lowest frequency of F0 or PF, (D1) duration from the start of the vocalization to the highest frequency value of F0 or PF, (D2) duration from the highest frequency of F0 or PF to the end of the vocalization, and (PD) plateau duration (when the frequency of F0 or PF did not vary). The number of pulses was measured using oscillograms for sounds that presented stretches with regularly spaced pulses (e.g., coo-call, purr, snort, adult and cub growls, scream, and scream-gurgle), and for sounds that presented a large number (>10) of pulses, we estimated the number of pulses by dividing the duration of pulsed stretches by the inter-pulse interval within that stretch. The sound parameters are presented as the mean and standard deviation (SD) of the mean or median and its respective ranges. Since we did not estimate the distance from which the subjects were recorded, it was not possible to measure amplitude parameters. However, we were able to describe some sound characteristics, such as relative intensity, by considering observer perceptions at the time of sound acquisition in the field. Sound types that were already known were named according to the first descriptions

elaborated by Duplaix (1980), while newly identified sounds were named by considering the acoustic characteristics and behavioral context in which they were emitted. Spectrogram and oscillogram figures were produced with R software using the *spectro* function in the *seewave* package (Sueur *et al.*, 2008).

D. Statistical analyses

All statistical analyses were performed using R 2.13 Software (R Foundation for Statistical Computing, 2011). The vocal repertoire of giant otters was derived from a continuum, with transitions, gradations and combinations among different sound types. Classifying the sounds occurring within this kind of complex communication system is a major challenge. Therefore, we used statistical methods to test for significant differences among the 15 discrete sounds types classified according to visual inspections of spectrograms and by measuring 13 structural characteristics (Appendix), and the behavioral context in which the sounds were emitted following studies of other mustelid species (McShane *et al.*, 1995; Wong *et al.*, 1999; Lemasson *et al.*, 2014). We standardized the acoustic parameters by columns and rows using the *decostand* function with the *total* method in the Vegan package (Oksanen *et al.*, 2013) and used a nested nonparametric multivariate permutational analysis of variance (PERMANOVA, age categories nested within sound types) to identify differences among sound types. We used the PERMANOVA analysis with 1000 permutations, which permutes the distance matrix (Manhattan method) of acoustic parameters, through the *adonis* function in the Vegan package.

A linear discriminant analysis (LDA) was carried out to estimate the distinctiveness between sound types, using the package MASS (Venables and Ripley, 2002). We applied the first step of LDA with a sorted (training) subset of 50% of the data. The remaining (validation) subset of data was used to evaluate the accuracy of classification based on equations derived from the training subset. The percentage of correctly classified cases indicates the effectiveness of discriminant function in distinguishing groups (vocalization type). We only used four variables to estimate the LDA among sound types (PF, Q3, FD, PU), since the other variables did not conform to the linearity assumptions of the analysis (Venables and Ripley, 2002). These included variables linked to the structure of the vocalizations and may reflect the emotional state of mammals (Briefer, 2012).

Because some of the sound types were expected to be subdivided between age categories, we applied a PERMANOVA with 1000 permutations (*adonis,* Vegan package) to test for these differences. We then conducted a hierarchical clustering analysis taking into account these subdivisions. For this analysis, we used a Manhattan-distance matrix of the median values of the variables extracted from each sound type and the average linkage between groups (UPGMA). This analysis results in a dendrogram representing the similarity between sound clusters (Wong *et al.,* 1999).

A principal-coordinate analysis (PCoA) was carried out to ordinate the 13 acoustic variables of the 15 main sound types from the Manhattan-distance matrix. To avoid distortions of the configuration due to extreme points from the PCoA, we corrected 53.3% of the distances using the "extended" procedure available in the *stepacross* function

from the package Vegan. We used a PERMANOVA (1000 permutations, *adonis,* Vegan package) to test whether the main context associated with the emissions of sounds was statistically associated with the ordination of acoustic variables (i.e., the first three axis of the PCoA).

E. Relationship between mustelidae vocal complexity and sociability

The vocal complexity of mustelids was estimated by the number of vocal types used by each species. We assessed this information in original articles found in the Web of Science search engine (http://apps.webofknowledge.com), using the arguments "vocalization" and "mustelidae," vocalization and "mustela," vocalization and "otter," and combined information from the literature with the data on giant otters collected for this study. Mustelid sociability level was estimated as the mean number of individuals in a breeding group according to Johnson *et al.* (2000). We applied a Spearman correlation between vocal complexity and breeding group size to determine whether or not the communication systems of mustelidae species supports the social intelligence hypothesis.

III. RESULTS

We recorded 6246 vocalizations during 112 h of monitoring. The individual total emission rate was 11.4 sounds/h (Table I), and the frequency of individual sound types varied from the rarely emitted cub squeak (0.03 sounds/h) to the most frequent cub call (3.4 sounds/h). We included only 458 of the total recorded sounds for the repertoire analysis (379 from adults/subadults, 9 from juveniles, and 70 from cubs),

TABLE I. Individual emission rates (number of sounds/h) and proportions of giant otter vocalizations given in different behavioral contexts (CC, close contact; GR, grooming; SW, swimming; DE, within the den; SM, scent-marking; IS, isolation; BE, begging; WD, warning/defense; IN, inquiry; AL, alarm; IA, intraspecific agonistic encounter; and IE, interspecific encounter by adults (A), subadults (S), juveniles (J), and cubs (C) from six groups. *n* is the number of sounds recorded, (groups) refers to the number of groups that presented that particular sound type in its repertoire.

Sound	*n*(Groups)	Age class	Sound/h	Behavioral Context (%)											
				CC	GR	SW	DE	SM	IS	BE	WD	IN	AL	IA	IE
1. Cub call	1388 (6)	J/C	3.4	10					59	31					
2. Purr	1523 (6)	A/S	3.0	52	15	12		21							
3. Snort	781 (6)	A/S/J/C	1.4										9	5	2
4. Coo	584 (6)	A/S	1.1	51	9	14		26							
5. Coo-hum	322 (6)	A/S	0.7	72	9	12		5	2						
6. Scream	310 (5)	A/S	0.5						39		47		9	5	
6.1. Cub scream	43 (5)	C	0.2				1								
7. Hum	235 (6)	A/S	0.5	55	19	5		21							
8. Coo-call	197 (6)	A/S	0.3	64		8		12	16						
9. Hah	174 (6)	A/S	0.3									10			
10. Begging scream	149 (4)	A/S	0.3					10		58				3	
10.1. Cub begging scream	155 (3)	J/C	0.7							10					
11. Growl	149 (5)	A/S	0.3								74		2		2
11.1. Cub Growl	12 (1)	C	0.1				1								
12. Adult call	148 (6)	A/S	0.2						74				5	2	
13. Scream-gurgle	25 (3)	C	0.1				1								
14. High scream	25 (3)	A/S	0.1							10					
14.1. Cub high scream	11 (2)	C	0.05				1								
15. Squeak	15 (1)	C	0.03	10											
Total	6246		11.4												

because most of the recordings overlapped with sounds from motor boats and/or vocalizations of other species or non-focal giant otters.

The vocal repertoire of giant otters was classified as 15 discrete sound types (PERMANOVA: $F_{14,443} = 130.66$, $R^2 = 0.81$, $P < 0.001$), of which seven were emitted only by adults and subadults; one, by juveniles and cubs only; two, exclusively by cubs; and five, by all age categories. Linear discriminant analysis correctly classified 74% of the 15 sound types. The first two discriminant functions explained 92% of the variance in sound variables. The number of pulses was the variable that contributed most to the first discriminant function, while the difference between the highest and the lowest frequency of F0 or PF (FD) was the most important variable in the second discriminant function.

Some of the main sound types could be subdivided into two subtypes, depending on the age of the sender, resulting in a total of 19 distinct sound subtypes (Fig. 3). The begging scream of adults/subadults and cubs/juveniles differed (PERMANOVA: $F_{1,19} = 3.35$, $P = 0.016$), but accounted for little of the variance in the data ($R^2 = 0.15$), so it was described as a single type within the repertoire. The cub growl differed from adult growls (PERMANOVA: $F_{1,25} = 14.53$, $P < 0.001$), but the difference explained a relatively low proportion of the variance in the data ($R^2 = 0.37$), and considering that the cub sound was very similar aurally to the adult growl, we considered them to be the same sound type. The high scream of cubs and adults (PERMANOVA: $F_{1,12} = 0.78$, $P = 0.536$) did not differ, although the high scream of some adults had nonlinear components. The adult/subadult and cub screams also did not differ statistically (PERMANOVA: $F_{1,27} = 1.35$, $P = 0.232$).
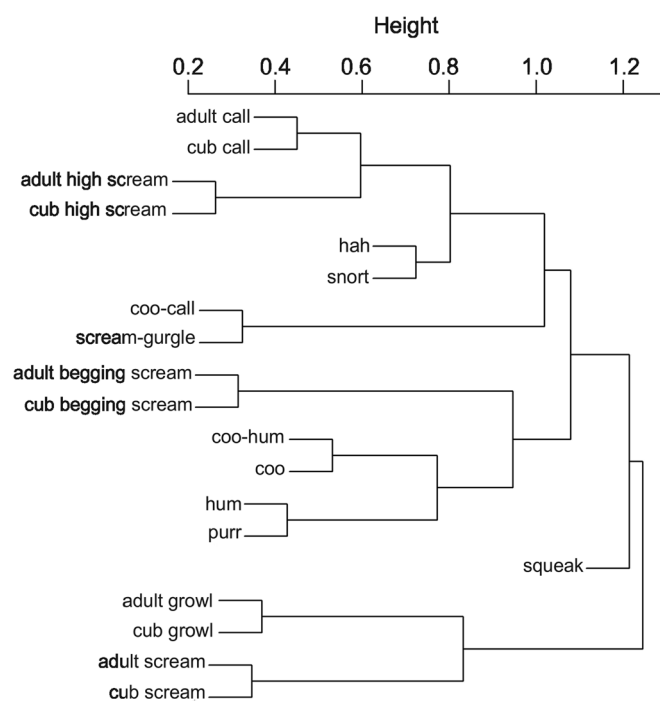

FIG. 3. Dendrogram of the hierarchical-cluster relationship of the 19 sounds ($n = 458$ vocalizations) emitted by giant otters distributed in nine groups in the Southern Pantanal, from November 2009 to June 2011. *Height represents a vector of the distances between merging clusters at successive stages, with shorter end branches indicating greater similarity of sound types.

A. Vocal repertoire and behavioral context

1. Coo

The coo is a discrete harmonic sound (Fig. 4) produced by adults and subadults with the mouth closed and was heard only at close range (to approximately 10 m) at a rate of 1.1 sounds/h (Table I). The average coo duration was 0.36 (SD = 0.11 s), with two harmonic parts or notes and visible pulses in part of or throughout the entire harmonic segment (Appendix; Table II). This chevron-shaped double-note sound was emitted mainly during close-contact episodes (51%, $n = 290$), especially when adults were caring for cubs, but also during scent-marking events (26%, $n = 148$). Adults cooed when they met while swimming (14%, $n = 80$), sometimes touching noses, and before changing their activity or leaving the site. Coos were also emitted during grooming sessions (9%, $n = 51$).

2. Coo-hum

This low frequency sound was emitted by adults and subadults at a rate of 0.7 sounds/h (Table I) with the mouth closed, and can be described as a combination of the coo and the hum (Fig. 4) sounds. The coo-hum is a harmonic sound with at least three visible harmonics and a mean call duration of 0.2 s (SD = 0.09 s), with pulses (Appendix; Table II) during the entire sequence or in segments of the sound. Individuals produced coo-hums mainly during close-contact events (72%, $n = 226$), when they were swimming together (12%, $n = 38$), grooming (9%, $n = 28$) and scent marking (5%, $n = 16$), similar to the behavioral contexts in which coos were produced. However, this sound was also emitted when an adult called other individuals, independent of their ages, to come out of the den (2%, $n = 6$).

3. Coo-call

The coo-call is perceived as louder than coos and coo-hums, with an average duration of 0.44 (SD = 0.13) s, and was given by adults and subadults at a rate of 0.3 sounds/h (Table I) with the mouth partially closed. This sound seems to be a combination of the coo and adult calls (Fig. 4). It is characterized by an abrupt transition from an ascendant low-pitch harmonic and pulsed segment resembling a coo to a high-pitched and bell-shaped frequency modulated harmonic sound similar to the adult call and then reverts back to a descendant pulsed sound at the end of the vocalization. The middle part of this sound may have a plateau (median of 0.03 s, ranging from 0.01 to 0.2 s) with a constant frequency (Appendix; Table II). Coo-calls were emitted when an animal appeared to be in a state of high arousal, mainly during close-contact events (64%, $n = 124$). This sound was also used for calling to other members of the group (16%, $n = 31$), as well as during scent-marking events (12%, $n = 23$), and swimming (8%, $n = 15$).

4. Hum

The hum is a low frequency sound emitted by adults and subadults at a rate of 0.5 sounds/h (Table I) with the mouth closed. This sound had at least five visible harmonics (Fig. 4), lasting an average of 0.33 (SD = 0.19) s, with some segments of regular pulses (Appendix; Table II). *Hums* were heard more
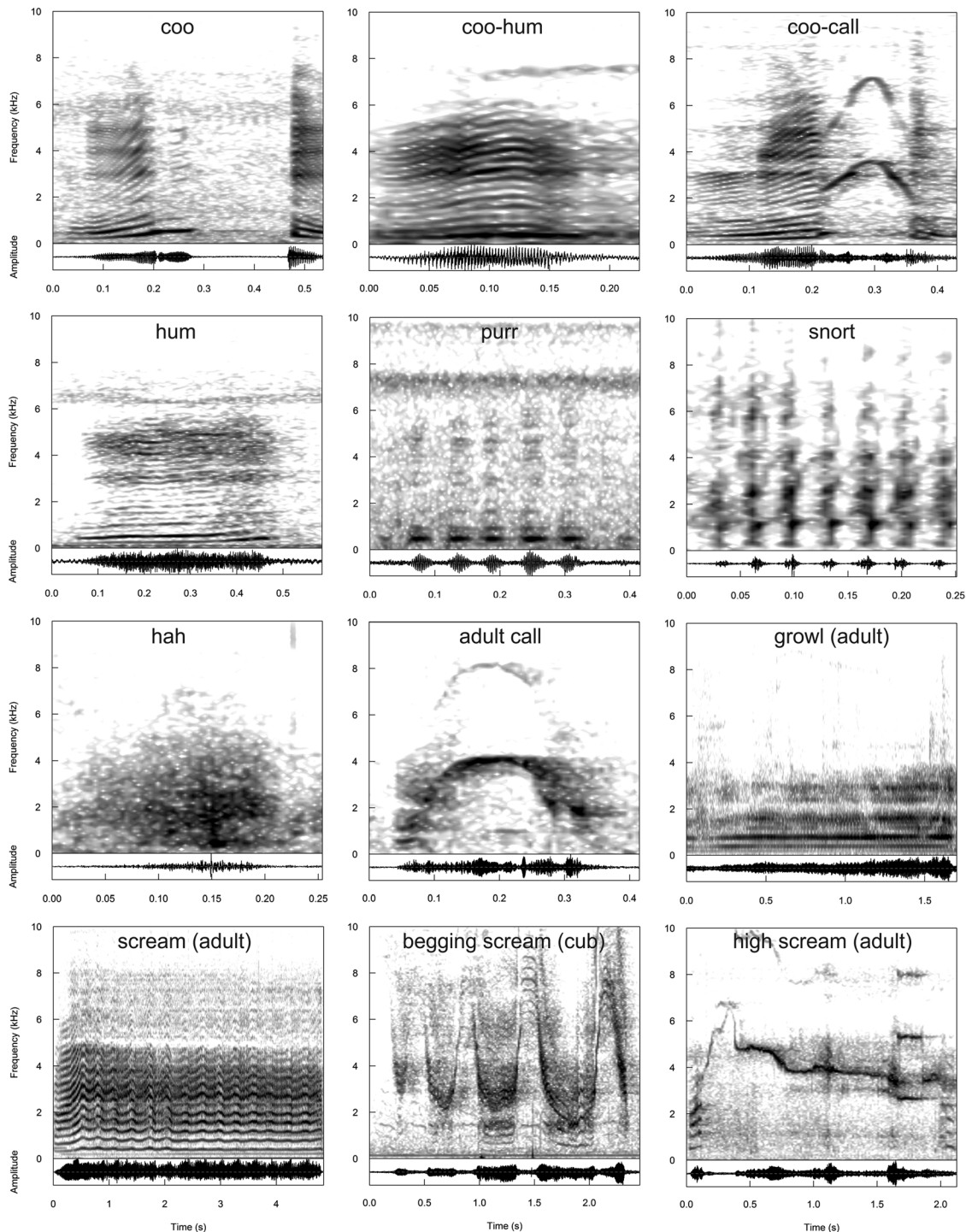
FIG. 4. Spectrograms (FFT: 512) and oscillograms (bottom) of vocalizations emitted by giant otters in the southern Pantanal of Brazil.

frequently during affiliative close contacts (55%, n = 123), followed by scent-marking events (21%, n = 47) and grooming (19%, n = 43). This type of sound was heard less often during swimming (5%, n = 11). The hum was commonly produced in combination with purrs [hum-purr, Fig. 5(a)] and growls.

5. Purr

The purr is a low frequency, harmonic and pulsed sound that was given by adults and subadults at a rate of 3 sounds/h

(Table I) with the mouth closed and has a nasal quality (Fig. 4). This sound had a call duration average of 0.54 (SD = 0.27) s and an average of 11.65 (SD = 5.25) pulses (Appendix; Table II). Purrs were the most frequent vocalizations (Table I), emitted during behavioral contexts similar those in which coos and hums were observed and were more frequently observed during close contact events (52%, n = 733). Gradations between the close contact coo, coo-hum, and coo-call sounds were commonly combined with hums and purrs [Fig. 5(b)]. Peters (2002) suggested that the

term purr is not adequate for similar sounds made by mustelids because it is not homologous to felid purring. However, considering the low intensity and rhythmic characteristics of this sound and the behavioral context in which giant otters emitted purrs, we maintained this term in describing the species' vocal repertoire.

6. Snort

The snort is an explosive, noisy, and pulsed sound, emitted during strong exhalations of air with the mouth partially open by all age classes, including 5-month-old cubs. While snorting in water, the animals commonly raised their throat out of the water (periscoping). The call duration of snorts showed an average of 0.27 (SD = 0.1) s, with a mean of 6.55 (SD = 2.35) pulses (Appendix; Table II). Snorts can be emitted as a single note or in double bursts. The snort burst was often louder when the animal was startled and may serve to alert other members of the group. Five formants were visible along the spectrogram of the snorts (Fig. 4). The snort was the second most often emitted sound type observed (1.4 sounds/h, Table I). This sound was usually given during alarm situations (93%, $n = 726$). Snorts were also emitted during intra-specific agonistic encounters (5%, $n = 39$) between different groups and inter-specific events (2%, $n = 16$) when the group faced caimans.

7. Hah

The hah is a noisy, atonal sound was produced by adults and subadults through exhalation and/or inhalation (Fig. 4). The hah is a short-lived sound with a mean duration of 0.16 (SD = 0.07) s (Appendix; Table II). Hahs were emitted mostly in low alarm situations within an inquiry context (100%, $n = 174$). In conflict situations, groups may emit sequential hahs combined with snorts. Hahs were emitted at a rate of 0.3 sounds/h and can transition into either alarm or affiliative sounds.

8. Adult call

The adult call is a harmonic, bell-shaped sound (Fig. 4), given by adults and subadults with the mouth partially open and at a rate of 0.2 calls/h (Table I). The mean call duration was 0.3 (SD = 0.1) s, with a plateau lasting from 0.01 to 0.26 s (median = 0.05 s, Appendix; Table II). This sound was emitted mainly when animals were calling to other group members (74%, $n = 120$), which sometimes elicited a response from another individual(s) that vocalized back with either calls or screams. During intra-specific agonistic encounters (21%, $n = 33$) adult calls were given in combination with screams and snorts. Adult calls were also emitted when individuals were startled (5%, $n = 8$). The ending of this sound became harsher and noisier or transitioned to a scream as the senders became more excited.

9. Growl

The growl is a low frequency, harmonic and pulsed sound given by adults and subadults. This sound is emitted with the mouth totally or partially closed and may present

amplitude modulation along the signal, with increasing energy toward the end of the sound (Fig. 4). The mean duration of this sound was 2.35 (SD = 1.71) s, and a high number of pulses and high values of the 3rd quartile frequency were observed (Appendix; Table II). Adults and subadults growled at a rate of 0.3 sounds/h (Table I). Growls were emitted mainly in warning and defense contexts (74%, $n = 107$), when the vocalizing individual was handling and eating a fish or it was directed toward another individual trying to steal it. While eating and growling, some individuals opened their mouths, producing a more intense sound with a slight increase in frequency. Startled individuals also growled as an alarm call (24%, $n = 35$) and during interspecific encounters (2%, $n = 3$) with caimans (*C. yacare*).

a. Cub growl. The cub growl is similar to the growl emitted by adults and subadults, and is a pulsed sound with a harmonic interval (Appendix; Table II). The mean duration was 0.46 s (SD = 0.25), with no frequency modulation. This sound was recorded from newborn cubs (1–3 months) inside of the den at a rate of 0.1 sounds/h.

10. Scream

The scream is a harmonic sound, which may present a wavering quality, and was emitted by adults and subadults, with the mouth open, at a rate of 0.5 sounds/h (Table I). This sound has some pulsed segments (Appendix; Table II), a mean duration of 0.93 s (SD = 0.41) and at least 11 visible harmonics (Fig. 4). Screams were emitted mainly during fishing events (47%, $n = 145$), and apparently served as a warning call. An individual that had caught a fish (especially if the fish was large) usually screamed with the prey in its mouth or in its forepaws. This sound was also emitted by giant otters that were caught trying to steal a prey item from another group member, and was usually answered with growls. When the motivation of an individual sender appeared to be more intense, screams showed chaotic components toward the end of the signal [Fig. 5(c)] or the scream merged into a begging scream. Screams were also emitted when individuals called to each other (39%, $n = 121$). For instance, individuals screamed to get cubs to come out of the den, or if an individual was not keeping up with the rest of the group during traveling events, where the individual may scream as a signal for other group members to wait up and may be answered with screams by other individuals. Moreover, individuals screamed (9%, $n = 28$) when startled, apparently as an alarm call for others. Screams may also become harsher in hostile situations, such as during intra-specific agonistic encounters (5%, $n = 16$) when almost all members of the group screamed in a chorus interspersed with abrupt calls.

a. Cub scream. The cub scream is a harmonic sound, similar to the adult scream, and was emitted by young cubs within the den at a rate of 0.2 sounds/h (Table I). Cub screams presented pulsed segments with a mean duration of 0.81 (SD = 0.44) s (Appendix; Table II).

11. Begging scream

The begging scream was emitted by adults and subadults and is similar to the scream, but with a highly modulated tonal frequency component along parts of the signal or throughout the entire sound. The begging scream was given by opening and closing the mouth and during states of high-intensity motivation. The mean begging scream duration was 1.21 s (SD = 1.03) and presented a higher peak frequency than that of a regular scream (Appendix; Table II). The begging scream was emitted at a rate of 0.3 sounds/h (Table I) in a begging context during fishing events (58%, $n = 86$) and during agonistic encounters (32%, $n = 48$). Individuals sometimes screamed while scent marking (10%, $n = 15$), probably in response to the scent of an intruder.

a. Cub begging scream. The cub begging scream (Fig. 4) was emitted by both cubs and juveniles, at a rate of 0.7 sounds/h, when begging for fish ($n = 155$).

12. High scream

The high scream is a harmonic sound given by adults and subadults, with the mouth open. The median call duration of adult high screams was 0.94 s (ranging from 0.36 to 2.25 s, Fig. 4). Unlike the regular scream (described in Sec. III A 10), the peak frequency values of high screams were found for the fundamental frequency (F0) (Appendix; Table II). This sound showed nonlinear phenomena, including subharmonics and biphonation at irregular time intervals. High screams were heard only in the context of five fishing events (emission rate = 0.1 sounds/h, $n = 25$), when an individual begged for a fish from another group member. High screams were often combined in a continuous sequence with screams.

a. Cub high scream. The cub high scream was recorded from young cubs (1–3 months) at a rate of 0.05 sounds/h (Table I). This sound showed at least three visible harmonics and presented a median duration of 0.46 s (ranging from 0.29 to 0.95 s, Appendix; Table II). It was recorded when cubs were inside the den and sometimes displayed a gradation distinct from cub screams [Fig. 5(d)].

13. Cub call

The cub call is a high pitched and loud sound emitted by individuals ranging from 2 to 9 months of age at a rate of 3.4 sounds/h, with the mouth open (Fig. 6). Cub calls were frequency modulated with a mean duration of 0.35 s (SD = 0.15) and sometimes showed a flat frequency plateau at variable intervals (median 0.03 s, ranging from 0 to 0.34 s, Appendix; Table II). This sound was mainly given when cubs were calling to other individuals (59%, $n = 811$), typically when they were separated from the group. Cubs also used this type of sound to beg for fish (31%, $n = 426$) during fishing sessions. These calls may have a harsher ending or
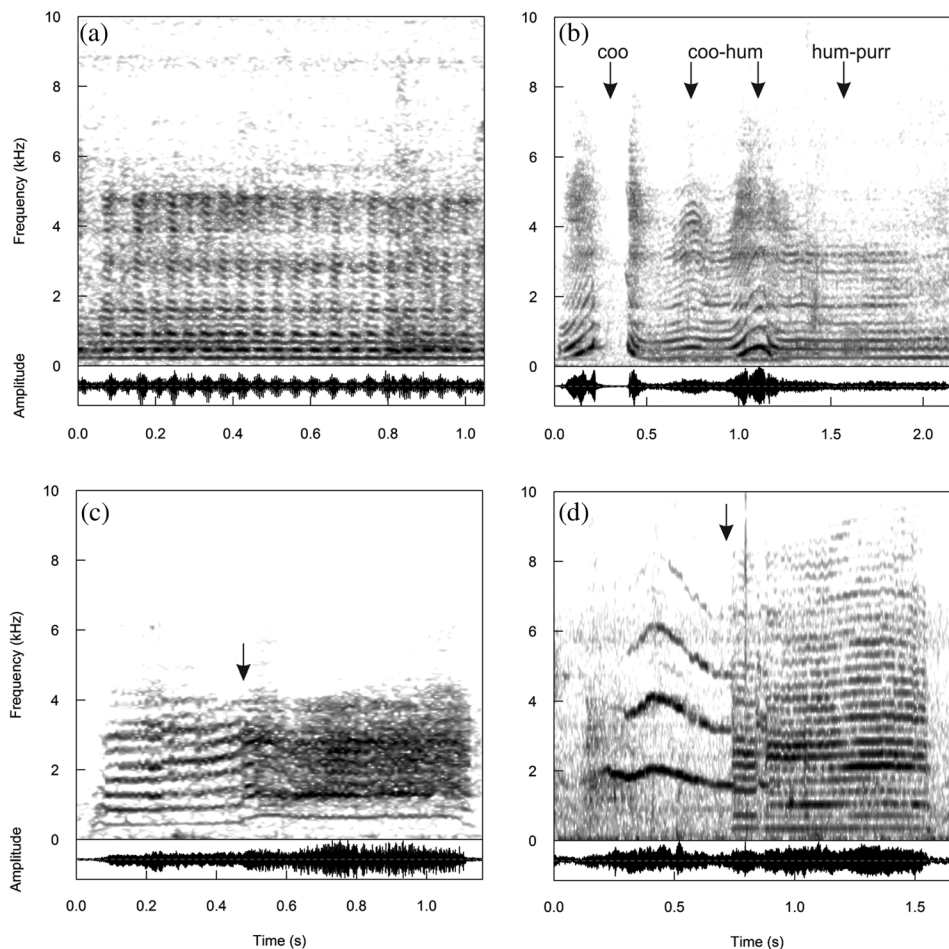

FIG. 5. Spectrograms and oscillograms (bottom) of vocalizations emitted by giant otters in the southern Pantanal of Brazil: (a) combination of hum and purr sounds (hum-purr, FFT = 1024), (b) gradation among affiliative sounds (coo, coo-hum, and hum-purr, FFT = 1024), (c) adult scream with a harsh, noisy ending (arrow indicates the transition, FFT = 512), (d) transition between cub high scream and cub scream (arrow indicates the transition, FFT = 1024).
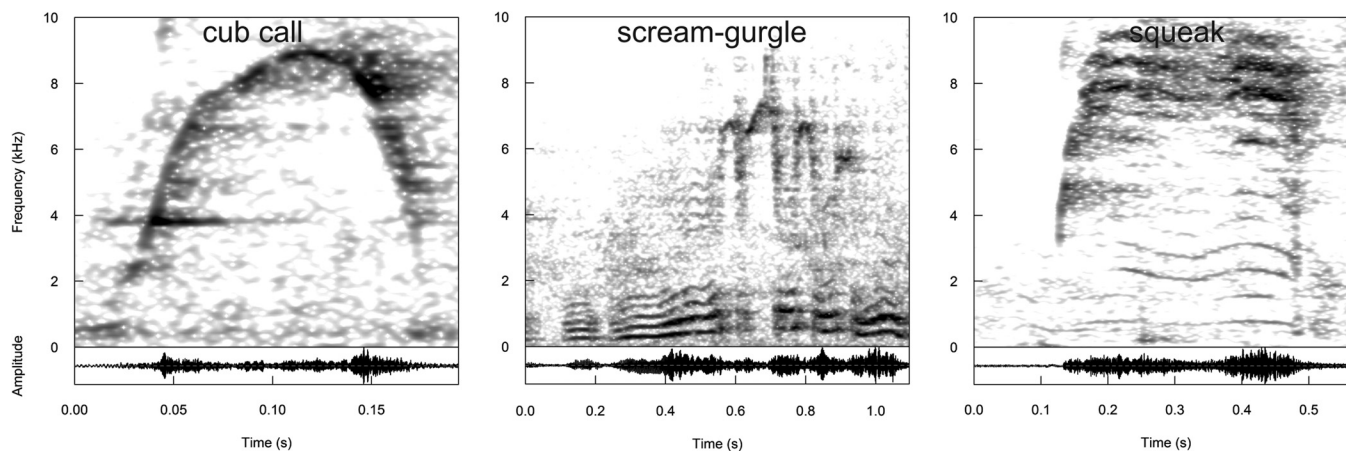
FIG. 6. Spectrograms (FFT = 512) and oscillograms (bottom) of vocalizations emitted by giant otters in the southern Pantanal of Brazil.

merge into a longer and high-frequency modulated begging scream when given by an individual in a more excited state. Cubs also emitted this call when being cared for by adults (10%, $n = 137$) in close-contact situations.

14. Scream-gurgle

The scream-gurgle was emitted by young cubs at a rate of 0.1 sounds/h. This harmonic sound presented a mean duration of 1.01 s (SD = 0.1), begins with a pulsed scream (Appendix; Table II) and ascends to a high-frequency interval, comprising four to five bell-shaped frequency modulated parts interspersed by short screams (Fig. 6). Scream-gurgles were given by young cubs from inside the den, while other cubs vocalized frequently with screams and high screams in the background. All scream-gurgles were recorded when a lactating female was in the den. On one occasion, cubs were observed emitting scream-gurgles while suckling from the female, which was lying near the den entrance.

15. Squeak

The squeak is a harmonic sound with an emission rate of 0.03 sounds/h that was recorded only in 2-month-old cubs from one group. The mean duration of squeaks was 0.44 (SD = 0.1) s, with a peak frequency of 8.38 (SD = 0.65) kHz (Fig. 6, Appendix; Table II). This sound was given during close contact events, while adults were caring for cubs, also emitting purrs, coos, and hums in the background.

The PCoA analysis resulted in three axes that accounted for 56% of the variation among sounds types, with 27.7% of the variation represented by the first axis; 17.1%, by the second axis; and 11.2%, by the third axis. Axis 1 had the highest loadings for the D2 (−0.686), D1 (−0.573), and PU (−0.536), and axis 2 had the highest loadings for FD (0.675), PU (−0.388), and PD (−0.328), while PU (0.377), D1 (−0.353), and FD (0.302) presented the highest loadings on the third axis (Fig. 7).

Although there is some overlap between fearful and friendly contexts (Fig. 7), the behavioral context of sound types was significantly associated with the ordination of acoustic variables provided by the three axes of the PCoA (PERMANOVA: $F_{6451} = 121.7$, $R^2 = 0.62$, $P < 0.001$).

Digital audio files of all the sound types described above are available at http://ppbio.inpa.gov.br/knb/metacat?action=read&qformat=ppbio&sessionid=0&docid=naman.540.1.

B. Relationship between mustelidae vocal complexity and sociability

We compiled published information on the repertoire size of 15 species of mustelids (Appendix; Table III). Adding our results to this list, we found a strong correlation between the repertoire size and the mean breeding group size of these mustelids ($\rho = 0.67$, $P < 0.01$).

IV. DISCUSSION

The vocal repertoire of giant otter groups in this study comprised 15 main sound types, usually emitted in different behavioral contexts. Discrimination of sounds, including information about the age category of the sender, resulted in a total of 19 sound subtypes. Although statistically and structurally different, some sound types, such as coos could be considered a single sound type because of similarity in the contexts in which these sounds are emitted. Duplaix (1980) described nine of these sounds qualitatively for giant otters in Suriname. Bezerra et al. (2010) presented acoustic measurements of five known sounds (snort, hah, scream, purr and cub call) recorded from five individual giant otters in Jaú National Park, Amazonas, Brazil. Machado (2004) identified nine sound types emitted by captive giant otters and free-ranging groups in the Balbina Hydroelectric reservoir in the Brazilian Amazon and described three new sound types recorded in the captive animals (buck, humhum, and a sound emitted by a resting adult female). The statistical methods applied here allow for a more objective classification of call types, resulting in a more robust means of measuring the size of the giant otter vocal repertoire.

In our study, the purr was the most frequently emitted sound in adults, followed by the snort, while the cub call was the most frequently emitted vocalization by cubs. Purrs have been described in the vocal repertoires of many mammals

(Peters, 2002) and are commonly classified as an affiliative close-contact sound (Sieber, 1984; Wong et al., 1999). Giant otters emitted purrs in intra-group close-contact events and when individuals were engaged in group activities, such as scent marking or swimming. The emission of purrs by giant otter groups in Suriname was found to be rare, as Duplaix (1980) recorded this sound only when adults were caring for young cubs, and observed that purrs were replaced by hums and coos as the cubs matured. However, Bezerra et al. (2010) recorded purrs emitted by a giant otter group in the Amazon but did not mention hums or coos, which were relatively common in our study (emission rate, hum = 0.5 sounds/h and coo = 1.1 sounds/h). Snorts, hahs, screams and cub calls seem to be common vocalizations in the repertoire of giant otters and have been described by many authors (Duplaix, 1980; Machado, 2004; Staib, 2005; Bezerra et al., 2010). Call-emission rates may also change among giant otters from different localities and could be a consequence of differences in sampling effort and recording methodology, as well as being influenced by environmental features, learning, or genetic variation among clades (Bradbury and Vehrencamp, 1998; Wilson, 2000).

The vocal repertoire of a species that includes a variety of sounds, may serve to transmit a corresponding number of messages (Bradbury and Vehrencamp, 1998). The giant otter snort is a sound type also found in the repertoire of other mammals (Sieber, 1984; Wong et al., 1999) and that is commonly emitted in alarm situations. In giant otters, more energetic snorts (with increasing amplitude) cause an immediate response from group members, which usually run to the water and submerge. The atonal hah has been suggested to signify some sort of inquisitive behavior (Duplaix, 1980), and is similar to the hiss sound commonly given in aggressive and fearful contexts by sea otters (McShane et al., 1995) and other mustelids (Huff and Price, 1968; Farley et al., 1987; Wong et al., 1999). Screams and harmonic sounds are common in the repertoires of many species (McShane et al., 1995; Wong et al., 1999; Fitch et al., 2002) and may provide identity information, as was recently documented for contact calls in giant otters (Mumm et al., 2014) and Aonyx cinerea (Lemasson et al., 2013), and have an important function for group cohesion. Additionally, some physical features of sounds, such as the presence of formants in the snorts and the fundamental frequency of harmonic sounds, may be considered an honest indication of body size and individual identity (McShane et al., 1995; Sousa-Lima et al., 2002; Fitch et al., 2002), and should also be considered in studies of acoustic individuality in the species.

Nonlinear phenomena, such as chaotic structures, biphonations and subharmonics, were observed in adult screams and high screams. These acoustic phenomena originate from the intrinsic properties of the vibrating components of the larynx (Fitch et al., 2002), but may also be produced as a result of systemic infection or diseases in the vocal tract (Riede et al., 1997). The presence of nonlinear components has been observed in many other mammalian vocalizations (Fitch et al., 2002; Sousa-Lima et al., 2002; Blumstein et al., 2008) and may be another means of achieving individual recognition. However, in some mammals, the presence of

non-linearity in sounds may indicate the arousal state of individuals (*Marmota flaviventris*, Blumstein et al., 2008; *Ailuropoda melanoleuca*, Briefer, 2012).

The main behavioral contexts of sound types were significantly associated with acoustic variables. The main variables of the three axes of the PCoA were related to the duration and shape of the sound (D1, D2, FD) and the number of pulses (PU). According to Briefer (2012), there is a positive relationship between arousal level and some acoustic variables, especially source-filter parameters (e.g., F0 range, F0 contour) that reflect the structure of the vocalization and the mode of production. This observation is consistent with the motivational structure (MS) model, which hypothesizes that vocalizations given in aggressive and hostile situations are low frequency and noisy, and that sounds given in fearful or friendly contexts are high frequency and tonal (Morton, 1977; August and Anderson, 1987). In the giant otter vocal repertoire, alarm, inquiry and warning sounds were noisier and occurred at lower frequencies, while calls and some scream types were harmonic and had higher frequencies. In more excited motivational states, the endpoint of adult calls and screams becomes harsher and noisier, indicating a high degree of individual hostility, as suggested by Morton (1977). The harmonic coo sounds, given mainly in close contact situations, changed from a lower intensity coo with a silent interval to a combination coo-hum and, in a more excited state, to a coo-call with a high frequency interval, which may elicit proximity in affiliative contexts. Although there is much overlap between fearful and friendly contexts (August and Anderson, 1987), the vocal repertoire of giant otters seems to be consistent with the MS hypothesis and may reflect the arousal state of individuals.

Transitions and gradations may increase the variability of sound combinations and convey more information than discrete signals (Wilson, 2000). The vocal repertoire of giant otters can be classified as a continuum, presenting graded sounds that were common during affiliative close contact and in more excited and agonistic events, as also observed in the repertoire other social mustelids (McShane et al., 1995; Wong et al., 1999; Lemasson et al., 2014). The combination of sounds, as in the hum with the affiliative purr, or the hum with the aggressive growl, probably increases the amount of information to be decoded (Crockford and Boesch, 2005). During agonistic encounters, screams became modulated and turned into abrupt calls, generating a long, harsh chorus (Ribas and Mourão, 2004; this study). During some excited fishing events, as well as during suckling, screams and cub calls graded into begging screams or high screams, which may reflect the arousal state of those individuals, as it does in sea otters (McShane et al., 1995). This high correlation between vocal complexity and sociability in mustelids suggests that the information compiled for this group supports the social intelligence hypothesis of Freeberg et al. (2012). Mustelids present a diverse and flexible social organization, with both interspecific and interpopulation variation (Johnson et al., 2000). Scent-marking is believed to be the primary form of communication in mustelids and is highly related to their social organization (Hutchings and White,
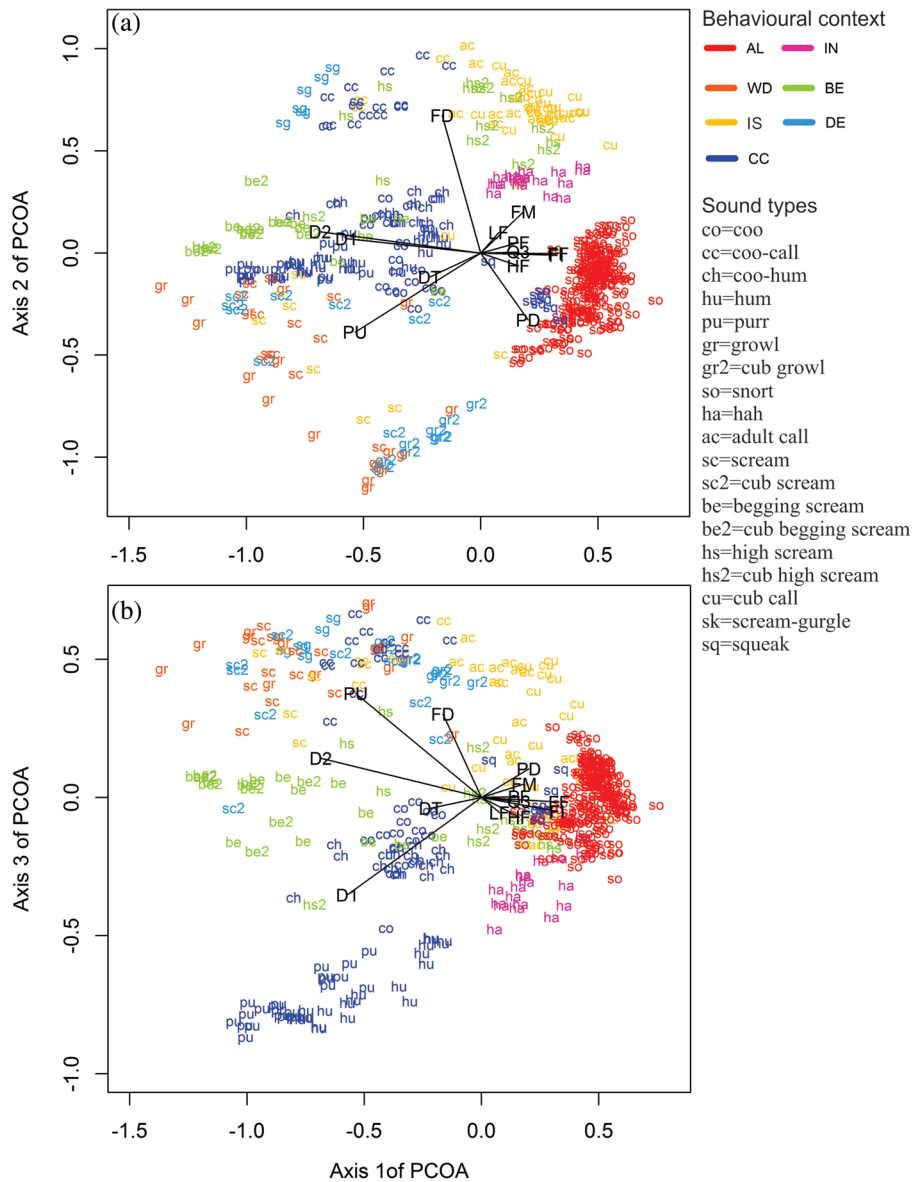
FIG. 7. Biplots of the relationship between the first and second axes (a) and the first and third axes (b) of the principal coordinate analysis (PCoA) of 19 sounds (see legend beside the graphs) vocalized by giant otters in different behavioral context (AL, alarm; IN, inquiry; WD, warning/defense; BE, begging; IS, isolation; DE, within den; CC, close contact) represented by different colors (see legend above the graphs). The capital letters (in black) indicate the sound features analyzed (CD = call duration, LF = lowest, and HF = highest frequencies of the sound, PF = peak frequency of the entire sound, Q3 = 3rd quartile frequency, PU = number of pulses of the sound, FI = initial value of F0 (for harmonic sounds) or of the peak frequency (for non-harmonic sounds), FM = maximum value of F0 or PF, FF = final F0 or PF, FM = maximum frequency of F0 or PF, FD = difference between the highest and the lowest frequency of F0 or PF, D1 = duration from the start of the vocalization to the highest frequency value of F0 or PF, D2 = duration from the highest F0 or PF to the end of the vocalization, and PD = plateau duration (when F0 or PF did not vary).

2000). However, the details of vocal communication in most species is still unknown and may be useful to understand the social complexity of the group.

Giant otter vocal repertoires represent a good example of how communication is intrinsically linked with sociality (Freeberg *et al.*, 2012). The large size (15 sound types) and the presence of gradations, transitions and combinations in the vocal repertoire of giant otters reflects their high degree of sociality, as previously suggested (Duplaix, 1980, 1982) and observed in mustelids and other social mammals (*Canis lupus*, Schassburger, 1993; *E. lutris*, McShane *et al.* 1995; *M. meles*, Wong *et al.*, 1999; *Pan troglodytes*, Crockford and Boesch, 2005; *A. cinerea*, Lemasson *et al.*, 2014). The variety of sound types and possible combinations, as well as the function of nonlinear components in giant otter vocalizations, should be considered in future acoustic studies, as these components may indicate an important mechanism in the communication system of the species.

APPENDIX

TABLE II. Descriptive statistics [$X \pm$ SD or median (minimum–maximum ranges)] of sound types emitted by giant otters from six groups monitored from September 2009 to June 2011 in the Southern Pantanal, Brazil. N represents the number of sounds used for acoustic measurements, and the number of giant otters groups included in analyses of each sound type is given in parentheses. (Sound: Co = coo, Cc = coo-call, Ch = coo-hum, Hu = hum, Pu = purr, Gr = growl, Gr2 = cub growl, So = snort, Ha = hah, Ac = adult call, Sc = scream, Sc2 = cub scream, Be = begging scream, Be2 = cub begging scream, Hs = high-scream, Hs2 = cub high-scream, Cu = cub call, Sk = scream-gurgle, Sq = squeak; Variables: CD = call duration, LF = lowest and HF = highest frequencies of the sound, PF = peak frequency of the entire sound, Q3 = 3rd quartile frequency, PU = number of pulses of the sound, FI = initial value of F0 (for harmonic sounds) or of the peak frequency (for non-harmonic sounds), FM = maximum value of F0 or PF, FF = final F0 or PF, FM = maximum frequency of F0 or PF, FD = difference between the highest and the lowest frequency of F0 or PF, D1 = duration from the start of the vocalization to the highest frequency value of F0 or PF, D2 = duration from the highest F0 or PF to the end of the vocalization, and PD = plateau duration (when F0 or PF did not varied), *temporal units in seconds (s), frequency units in kHz).

Call	N	CD	LF	HF	PF	Q3	PU	FI	FF	FM	FD	D1	D2	PD
Co	15	0.36 ± 0.11	0.18 ± 0.05	5.29 ± 0.94	0.45 ± 0.05	0.61 ± 0.26	109.67 ± 29.19	0.27 ± 0.06	0.33 ± 0.05	0.52 ± 0.06	0.25 ± 0.06	0.15 ± 0.06	0.07 ± 0.03	0.16 ± 0.09
Cc	18	0.44 ± 0.13	0.16 ± 0.04	4.98 ± 1.43	0.5 (0.3–4.09)	2.89 ± 1.38	77.22 ± 33.55	0.26 ± 0.1	0.34 ± 0.1	4.32 ± 1.14	4.06 ± 1.14	0.26 ± 0.12	0.13 ± 0.07	0.03 (0.01–0.2)
Ch	20	0.2 ± 0.09	0.17 ± 0.03	4.75 ± 1.31	0.44 ± 0.08	0.51 (0.39– 3.66)	98.7 ± 45.88	0.25 ± 0.04	0.27 ± 0.06	0.43 ± 0.08	0.18 ± 0.08	0.11 ± 0.07	0.08 ± 0.04	0
Hu	20	0.33 ± 0.19	0.09 ± 0.07	4.84 ± 1.18	0.43 ± 0.08	0.62 (0.43–4.1)	80.4 ± 48.2	0.23 ± 0.04	0.26 ± 0.06	0.27 ± 0.07	0.04 ± 0.07	0.26 ± 0.14	0	0
Pu	23	0.54 ± 0.27	0.09 ± 0.07	2.35 ± 1.76	0.42 ± 0.07	0.52 (0.39–3.19)	11.65 ± 5.25	0.21 ± 0.01	0.21 ± 0.01	0.21 ± 0.01	0	0.54 ± 0.27	0	0
Gr	17	2.35 ± 1.71	0.12 ± 0.04	3.75 ± 0.8	0.39 (0.17–2.63)	2.16 ± 0.77	516.94 ± 339.27	0.2 ± 0.03	0.2 ± 0.04	0.22 ± 0.04	0.02 (0–0.1)	0.1 (0–1.97)	0.13 (0–4.23)	1.05 (0 to 3.22)
Gr2	10	0.46 ± 0.25	0.07 (0– 0.15)	1.29 ± 0.17	0.44 ± 0.02	0.47 ± 0.01	115.8 ± 63.62	0.22 ± 0.01	0.22 ± 0.01	0.22 ± 0.01	0	0.00	0.00	0.37 (0.17–0.93)
So	197	0.27 ± 0.1	0.16 ± 0.04	8.70 ± 1.29	1.47 ± 0.74	2.63 ± 0.67	6.55 ± 2.35	1.47 ± 0.75	1.77 ± 0.81	1.47 ± 0.74	0	0	0	0.27 ± 0.1
Ha	11	0.16 ± 0.07	0	4.38 ± 0.55	1.56 ± 0.63	2.31 ± 0.54	1	1.43 ± 0.49	1.03 ± 0.67	2.07 ± 0.23	0	0.16 ± 0.07	0	0
Ac	15	0.3 ± 0.1	0.75 ± 0.86	5.94 ± 1.47	4.42 ± 1.51	4.96 ± 0.86	1 ± 0	0.56 (0.27–4.15)	1.87 ± 1.32	5.94 ± 1.42	4.33 ± 1.95	0.14 ± 0.04	0.09 ± 0.05	0.05 (0.01–0.26)
Sc	20	0.93 ± 0.41	0.22 ± 0.09	6.57 ± 2.22	1.56 ± 0.64	2.60 ± 0.95	466.35 ± 202.72	0.35 ± 0.06	0.43 ± 0.07	0.48 ± 0.08	0.12 ± 0.09	0.27 ± 0.22	0.29 ± 0.26	0.23 (0–1.42)
Sc2	9	0.81 ± 0.44	0.19 ± 0.09	5.64 ± 2.34	1.18 ± 0.71	2.24 ± 0.87	268.22 ± 146.67	0.32 ± 0.07	0.34 ± 0.05	0.37 ± 0.05	0.05 (0–0.22)	0.09 (0–1.1)	0.31 ± 0.3	0.22 ± 0.09
Be	12	1.21 ± 1.03	0.13 ± 0.11	6.91 ± 1.52	3.13 ± 1.82	4.15 ± 1.1	1 ± 0	0.39 ± 0.1	0.36 ± 0.09	0.49 ± 0.09	0.1 (0–0.34)	0.25 ± 0.19	0.96 ± 0.92	0
Be2	9	2.65 ± 1.39	0.17 ± 0.08	7.76 ± 1.67	2.67 ± 0.87	3.69 ± 1.04	1 ± 0	0.33 ± 0.03	0.37 ± 0.04	0.48 (0.35–3.22)	0.43 (0.07–2.9)	0.43 ± 0.34	2.22 ± 1.38	0
Hs	4	0.94 (0.36–2.25)	1.41 ± 1.26	6.61 ± 1.17	4.04 ± 1.91	4.68 ± 1.33	1 ± 0	3.15 (0.39–6.09)	3.02 ± 1.88	6.31 ± 1.05	3.12 ± 2.69	0.22 ± 0.13	0.63 (0.2–2.13)	0 (0–0.07)
Hs2	10	0.46 (0.29–0.95)	1.72 ± 0.81	6.3 ± 2.29	3.29 ± 1.07	4.29 ± 0.77	1 ± 0	3.03 ± 1.71	2.83 ± 0.98	5.19 ± 1.96	2.16 ± 2.06	0.17 (0–0.64)	0.33 ± 0.19	0
Cu	27	0.35 ± 0.15	1.41 ± 0.46	9.95 (7.7–13.92)	8.02 ± 1.46	8.64 ± 0.99	1 ± 0	3.17 ± 2.12	5.54 ± 2.82	8.83 ± 1.92	5.66 ± 2.43	0.13 ± 0.06	0.14 ± 0.09	0.03 (0–0.34)
Sk	6	1.01 ± 0.1	0.15 ± 0.02	8.73 ± 1.18	0.75 ± 0.26	0.85 ± 0.16	227.17 ± 33.89	0.24 ± 0.03	0.33 ± 0.04	7.83 ± 0.9	7.59 ± 0.91	0.61 ± 0.15	0.40 ± 0.06	0
Sq	15	0.44 ± 0.1	0	18.3 ± 1.23	8.38 ± 0.65	8.74 ± 0.68	1 ± 0	0.52 ± 0.06	0.57 ± 0.06	0.72 ± 0.07	0.21 (0.06–0.8)	0.08 (0.06–0.1)	0.06 (0–0.24)	0.26 (0.2–0.5)

TABLE III. Vocal complexity (RS-repertoire size) and mean breeding group size (BG) of mustelids. *Data available in Johnson *et al*., 2000.

Species	RS	BG*	Reference for RS
Aonyx cinérea	7	12	Lemasson *et al*., 2014
Enhydra lutris	10	6	McShane *et al*., 1995
Ictonyx striatus	8	1	Channing and Rowe-Rowe, 1977
Lontra canadenses	4	1	Almonte, 2011
Lutra lutra	7	3.5	Gnoli and Prigioni, 1995
Lutrogale perspicillata	6	2	Duplaix, 1982
Martes americana	6	1	Belan *et al*., 1978
Meles meles	16	4.65	Wong *et al*., 1999
Mustela erminea	2	1	Farley *et al*., 1987
Mustela eversmanni	5	1	Farley *et al*., 1987
Mustela frenata	3	1	Farley *et al*., 1987
Mustela nigripes	4	1	Farley *et al*., 1987
Mustela nivalis	4	1	Huff and Price, 1968
Poecilogale albinucha	9	1	Channing and Rowe-Rowe, 1977
Pteronura brasiliensis	15	6	This study

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