

Individual and sex distinctiveness in bark calls of domestic chinchillas elicited in a distress context

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Animals obtain information about their social environment by means of communication signals, which provide relevant subtle cues for individual recognition. An important requisite for this process is the existence of larger between- than within-emitter signal variation. Acoustic signals are complex traits susceptible of variation in their spectral and temporal components, implying that signal distinctiveness can result from differences in single or various acoustic components. In this study, domestic chinchillas were induced to vocalize in a distress context to describe the acoustic characteristics of the bark calls, and to determine features that denote the potential value of this vocalization for individual and/or sexual recognition. The results demonstrate that the variation in spectral and temporal components of the bark calls of chinchillas elicited under a distress context is larger between than within individuals, suggesting the potential of these signals for distinctiveness between individual signalers, although the potential of this call type for sex distinctiveness is quite limited. These results combined with previous studies on auditory capabilities of chinchillas contribute to position this rodent as a valuable model species for studying auditory–vocal interactions. © 2015 Acoustical Society of America. [<http://dx.doi.org/10.1121/1.4929750>]

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I. INTRODUCTION

Animals obtain information about their social environment by means of communication signals, which provide relevant subtle cues for individual recognition (Bradbury and Veherencamp, 2011). As such, distinctiveness in acoustic signals may facilitate offspring recognition, hierarchy identification, sex discrimination, and mate choice (e.g., Robisson *et al.*, 1993; Blumstein *et al.*, 2004; Blumstein and Munos, 2005; Aubin *et al.*, 2007; Tibbetts and Dale, 2007; Vergne *et al.*, 2007; Levréro *et al.*, 2009; Pollard, 2011; Pollard and Blumstein, 2011). A requisite for these processes is the existence of larger between- than within-emitter signal variation, and also that receivers should be capable to discriminate between different signalers based on these differences (Blumstein *et al.*, 2004; Schibler and Manser, 2007; Pollard, 2011).

Acoustic signals are complex traits susceptible of variation in their spectral and temporal components. Generally, spectral components are mostly determined by

the characteristics of the sound-producing organ, and temporal components are mainly affected by energetic and biomechanical constraints (e.g., Gerhardt and Huber, 2002; Greenfield, 2002; Fitch and Hauser, 2003). Because of these different determinants, signal distinctiveness can result from differences in single or various acoustic components (e.g., Aubin *et al.*, 2007; Hoffman *et al.*, 2012).

Alarm calls emitted by threatened individuals and distress calls emitted when animals are seized or captured are vocalizations typically produced under stressful situations such as predation risk. The main function of these call types is to warn other individuals and/or to induce a change in the predator's behavior (Caro, 2005). At first glance, the benefits associated to distinctiveness in these call types are not obvious, since fast responses to the warning of a dangerous situation irrespective of emitter assessment may result in an increment in receivers' fitness and, therefore, distinctiveness may not be favored by selection (Pollard, 2011). Nevertheless, individual distinctiveness may facilitate associative learning (Owren and Rendall, 2001) thereby allowing recognition of false alarms emitted by less reliable individuals and reducing the energetic costs of the behavioral response (Blumstein *et al.*, 2004; Blumstein and Munos, 2005; Pollard, 2011). In addition, distinctiveness may increase inclusive

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fitness by means of recognition of closely related individuals, and may also allow assessing the level of danger when several individuals call simultaneously (Blumstein and Daniel, 2004). Furthermore, distinctiveness in calls may indicate prey quality (e.g., the ability to escape), which could affect the behavioral response of predators (Laiolo *et al.*, 2004). Studies performed in different vertebrate species have shown distinctiveness in calls emitted under stressful situations (e.g., Rendall *et al.*, 2009; Schehka and Zimmermann, 2009; Matrosova *et al.*, 2011; Stoeger *et al.*, 2011), especially in social animals (Pollard and Blumstein, 2011).

Distinctiveness in vocalizations produced under stressful situations can be associated to different conditions such as sex, individual constitution, and age, and the distinctiveness may reside in different temporal and/or spectral variables (e.g., Blumstein and Daniel, 2004; Blumstein *et al.*, 2004; Blumstein and Munos, 2005; Matrosova *et al.*, 2011). For instance, in the gray mouse lemur (*Microcebus murinus*; Leliveld *et al.*, 2011), both frequency and temporal variables contribute to individuality of calls elicited under stressful situations. In the yellow-bellied marmot (*Marmota flaviventris*), although both spectral and temporal variables of alarm calls could provide individual distinctiveness, not all of these variables have the potential to provide cues about the age of individuals, and only spectral variables differ between sexes (Matrosova *et al.*, 2011). In partial contrast, speckled ground squirrels (*Spermophilus suslicus*) produce alarm calls having variation that can provide identity, however, only a few of these variables provide information about age and no components differ between sexes. Differences in distinctiveness can be associated to the degree of sociality of each species, an enhanced discrimination being likely beneficial in highly social species (Matrosova *et al.*, 2011). Although different groups of variables have the potential to provide distinctiveness at different levels, there could also be variation among taxa, rendering further studies on additional species necessary to improve generalizations about signal distinctiveness.

The chinchilla (*Chinchilla lanigera*) is a social South American hystricognath rodent that, in natural conditions, congregates in colonies of circa 100 individuals (reviewed in Spotorno *et al.*, 2004). Field observations suggest that is a monogamous species (Grau, 1993), where males can display behaviors of acceptance and care to the offspring. Individuals are philopatric, remaining for several years in small areas. There is sexual dimorphism in body size, females being larger than males. Natural predators include culpeo foxes (*Pseudalopex culpaeus*) and Magellan-horned owls (*Bubo magellanicus*) (reviewed in Spotorno *et al.*, 2004). Natural populations of this species are in drastic decline and, therefore, classified as critically endangered by the International Union for Conservation of Nature (IUCN) (D'Elia and Teta, 2008). In contrast, domestic chinchillas are highly abundant, being used mainly as pets and for peltry (Spotorno *et al.*, 2004). The domestic chinchilla has become an important model for studies of hearing, including anatomical, behavioral, and neurophysiological reports, which have documented remarkable auditory capabilities in this species (e.g., Daniel *et al.*, 1982; Azeredo *et al.*, 1999; Delano *et al.*, 2007; Delano *et al.*, 2008; Elgueta *et al.*, 2011; León *et al.*,

2012). Previous studies have reported that domestic chinchillas produce several call types, among which bark calls are produced when animals are frightened or seized. A potential function of this call is to alert other individuals about the occurrence of a threat (Spotorno *et al.*, 2004; Bartl, 2006; Hunyady, 2008). Although the evolutionary impact of domestication on the acoustic traits of this species is uncertain, the chinchilla is a social species and therefore we expect this call to have a potential for distinctiveness, allowing recognition of calling individuals. Here, we induced chinchillas to produce bark calls in a distress context (i.e., when animals are captured by predators or humans; Caro, 2005). We aimed to describe the acoustic characteristics of these signals and to determine acoustic features that denote their potential value for individual and/or sexual distinctiveness. As chinchillas have a high auditory capability and constitute a suitable model for studying acoustic communication, this information contributes to the knowledge in acoustic distinctiveness and is particularly relevant for future studies combining behavioral and physiological evidence.

II. METHODS

A. Animal maintenance

All chinchillas used in this study were sexually mature, i.e., between 1 and 2 years of age and were obtained from a local commercial husbandry for peltry where they are reared in standard conditions. Upon arrival in the laboratory, the animals were maintained individually in cages (40 cm × 40 cm × 50 cm) under inverted 12:12 h photoperiod (lights on at 20:00 h). Acoustic recordings were performed during daytime (between 08:00 and 20:00 h) and within two weeks of arrival in the laboratory. Animals were not acclimatized for a longer period of time because their readiness to vocalize decreases as they accustom to the facility at the university. All procedures involving chinchillas were approved by the local Committee of Bioethics (Comité de Bioética Animal #098 Facultad de Medicina, Universidad de Chile).

B. Acoustic recordings

Recordings of chinchillas' bark calls elicited in a distress context were performed in a sound-attenuated booth having walls and ceiling covered with 10-cm foam wedges, in sessions conducted during 2006, 2011, 2012, 2014, and 2015. Animals were recorded individually inside a metallic mesh cage (32 cm × 27 cm × 29 cm). Each individual ($n = 63$) was recorded during a 15 min session. To induce vocal behavior, subjects were gently touched by hand. During each year, the same experimenter conducted the stimulation of individuals. Calls were recorded with the microphone of a sound level meter [Brüel and Kjaer 2230 (Nærum, Denmark), frequency response: 20 Hz–20 kHz] connected to a digital recorder [Sony (Tokyo, Japan) TC D10 PRO II, TASCAM (TEAC Corporation, Montebello CA) DR-100 mkII] (sampling rate: 44 100 Hz, digitized at 16 bits). The acoustic recordings made with the Sony TC D10 PRO II recorder were digitized using a Power Mac G4 (Apple, Cupertino, CA) computer at the same sampling rate

and number of bits. The sound level meter microphone was positioned at 50 cm from the cage border. After acoustic recordings, body mass of animals was measured using an Ohaus-700 (Parsippany, NJ) series scale.

C. Vocalization analysis

The bark calls of chinchillas are composed of a series of pulses that vary in their spectral and temporal components (e.g., Hunyady, 2008; Fig. 1). In order to describe temporal parameters, we used Raven Pro 1.4 (Cornell Lab of Ornithology, Bioacoustics Research Program) to determine visually the number of pulses contained in each call. For each call, we made selections of the entire first and last pulses and also of their adjacent pulses, i.e., the second and the penultimate pulses. The selections of the first and last pulses were used to obtain the duration of these emissions and also of the entire call. In addition, the inter-pulse periods of the first and last pulses were obtained. Pulse period is strictly related to pulse rate as it corresponds to the time elapsed between the onsets of consecutive pulses (pulse rate = 1/pulse period). The selections were also used to obtain the mean power spectra of the first and last pulses with a custom-automated analysis implemented with the R (version 3.0.2; R Core Team, 2013) sound analysis package *seewave* (version 1.7.2; Sueur *et al.*, 2008). Frequency parameters were obtained with a fast Fourier transform and a Hanning window having a length of 2048 points, which yielded a frequency resolution of 21.53 Hz and a temporal resolution of 46.44 ms. This allowed to obtain the dominant frequency, i.e., the frequency with highest energy content, and other measurements describing the frequency energy distribution of mean power spectra: first, second, and third quartiles, inter-quartile range, skewness, i.e., power spectrum asymmetry, and kurtosis, i.e., power spectrum peakedness. We also obtained the spectral entropy of the first and

last pulses. The temporal entropy was obtained from the envelope. The total entropy (i.e., product of spectral and temporal entropy) of the first and last pulses was also obtained. Entropy values vary between 0 and 1, 1 being the highest entropy. In addition, to describe frequency variations within pulses, we computed the power spectra at the middle portions of the first, second, and last thirds of the first and last pulses. These spectra were used to obtain the dominant frequency and the fundamental frequency at the three time intervals within the first and last pulses. Only calls free from interference from sounds caused by the movement of the individual inside the cage were included in the analysis.

D. Statistical analysis

Only individuals with a minimum of eight clean calls recorded were included in the analysis, which is comparable to the number of calls used in former studies on the individual variation of vocalizations (e.g., Mathevon *et al.*, 1997; Bee *et al.*, 2001; Aubin *et al.*, 2007). This allowed analyzing 376 calls from 27 individuals (median = 12 calls; range: 8–31 calls). The resulting sample included 16 females (593 ± 72 g) and 11 males (551 ± 103 g).

Because different individuals were recorded during different years, prior to data pooling the effect of year was evaluated using a one-way analysis of variance. If original variables were not normally distributed (tested with Shapiro–Wilk normality test), variables were transformed and retested (see supplementary material I¹). If transformed variables were not normally distributed, we performed a Kruskal–Wallis test. The effect of year was not statistically significant for any variable measured (see supplementary material I¹).

Descriptive statistics of acoustic variables were calculated from individual means. Since not all individuals had a reliable tonal harmonic structure, the characteristics of the fundamental frequency were obtained only for a subset of

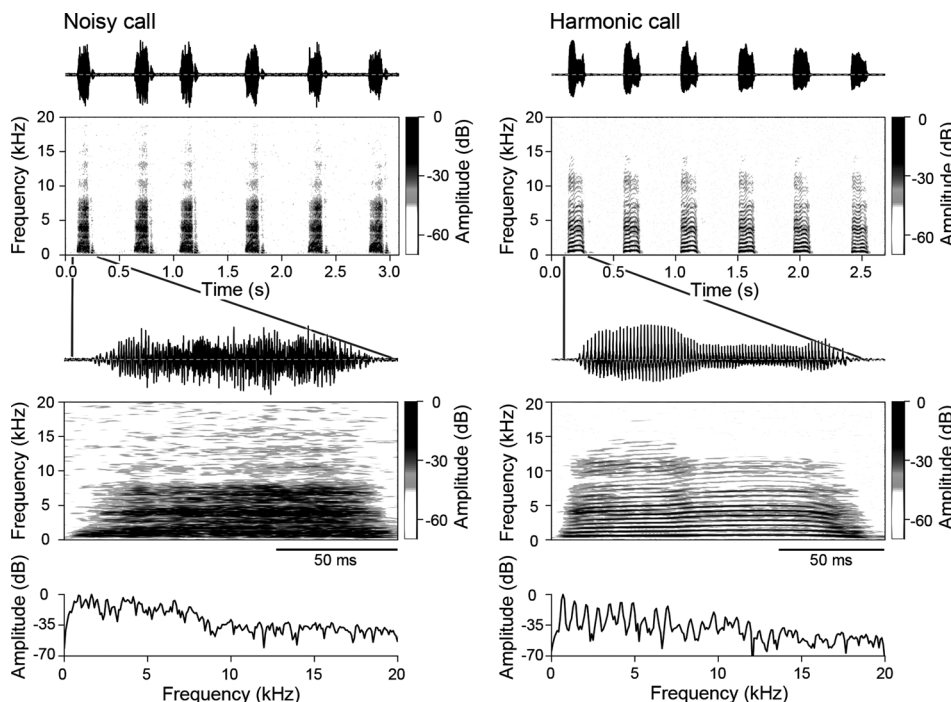


FIG. 1. Examples of chinchillas' bark calls elicited in a distress context. A non-harmonic or noisy call is shown on the left side and a harmonic call is displayed on the right side. In the upper part of the figure, oscillograms and spectrograms of complete calls composed by six elements are shown. In the lower part, expanded views of the oscillogram and spectrogram of the first pulse are shown, and the corresponding power spectra calculated at the middle portion of the first pulses are displayed at the bottom.

the individuals. This precluded the inclusion of the fundamental frequency in further statistical tests.

To determine the effects of body mass and sex on each variable, linear mixed-effects models were used. All calls were included in the analysis and individual intercepts were included as a random effect in order to account for data dependence (Pinheiro and Bates, 2000). The significance of the interaction and of the main effects was tested through likelihood ratio tests. Variables were log or square-root transformed in order to improve normality. This analysis was performed using the R (v. 3.0.2; R Core Team, 2013) library lme4 (Bates et al., 2014).

The potential for individual coding (PIC) and the potential for sexual coding (PSC) were estimated by calculating the ratio between the coefficients of variation between (CV_b) and within (CV_w) groups, where the group corresponded to individuals in PIC and to sex in PSC (e.g., Aubin et al., 2007). From these analyses, values larger than one indicate that a call characteristic is potentially distinctive. The significance of PICs and PSCs was assessed with Kruskal–Wallis tests (e.g., Aubin et al., 2007). Because our sample included individuals with different numbers of calls, a bootstrapped routine with 1000 iterations was implemented using R (version 3.0.2; R Core Team, 2013). In the case of PIC, eight calls obtained at random with replacement were included in each iteration. This number was used as it corresponds to the lowest number of calls produced by an individual to be included in the analysis. In the case of PSC, one call of each individual was randomly obtained (e.g., Aubin et al., 2007) and included in each iteration. Random samples were obtained with the R function “sample,” and though iterations all calls have the potential to be included in the analysis. This procedure allowed us to obtain the median of each coefficient and its confidence interval at 95%.

Backward stepwise discriminant function analysis (DFA) was performed to determine which were the most important variables contributing to distinctiveness at the individual and sex levels, and to determine to which extent the calls could be correctly classified to the corresponding group (i.e., individual and sex). In the case of individual discrimination, eight calls per individual were randomly obtained without replacement. In sexual discrimination, one call per individual was obtained. Prior to performing DFA, variables were normalized, centered, and scaled (Crawley, 2013). In order to avoid collinearity issues, highly correlated variables were eliminated from the analysis. To achieve this, Spearman correlations between pairs of variables were performed, and variables from a pair that yielded an absolute correlation value above or equal to 0.85 were eliminated. Backward stepwise variable selection was implemented with a tenfold cross-correlation having a correctness rate with a stop criterion of 5% using the “stepclass” function from the R library klaR (Weihs et al., 2005). This procedure consists in evaluating models differing in variable composition, finding out if the exclusion of a variable improves model performance. In addition, we assessed the predictive accuracy of call discrimination using a leave-one-out cross-validation procedure. This technique determines the accuracy of prediction of an undetermined sample based on discriminant

functions from DFA obtained with a data set excluding the sample to be assessed. This was performed under a bootstrapped routine with 1000 iterations using the same sampling procedure as for univariate analysis. We obtained the percent of correct classification and its confidence interval at 95%. Within each iteration, variables were normalized, centered, and scaled, potential collinear variables were excluded, and the model was obtained with backward stepwise variable selection. These analyses were performed using the R (v. 3.0.2; R Core Team, 2013) libraries MASS (Venables and Ripley, 2002) and klaR (Weihs et al., 2005).

III. RESULTS

A. General description of chinchillas' calls elicited in a distress context

The bark calls of chinchillas elicited in a distress context had a variable number of pulses, ranging from 2 to 17 pulses (median = 7 pulses). The duration of the entire call had a median of 3.5 s ($Q1 = 2.8$, $Q3 = 4.7$ s). The first pulse had a median of 165 ms ($Q1 = 133$, $Q3 = 188$ ms), and the last pulse had a median of 158 ms ($Q1 = 129$, $Q3 = 222$ ms), the corresponding pulse periods were 542 ms ($Q1 = 491$, $Q3 = 599$ ms) and 525 ms ($Q1 = 458$, $Q3 = 601$ ms), indicating that pulse rate ranged between 1.845 and 1.905 pulses/s (pulse rate = $1/\text{pulse period}$). Among the individuals that produced pulses with a reliable tonal structure, the fundamental frequency of the first pulse had a median starting value of 669 Hz ($Q1 = 534$, $Q3 = 773$ Hz), which tends to decrease toward the final part of the pulse. The last pulse can also have frequency modulations and had a lower overall fundamental frequency than the first pulse. The dominant frequency of the mean power spectrum of the first pulse had a median value of 1115 Hz ($Q1 = 684$, $Q3 = 1477$ Hz), indicating that generally it does not correspond to the fundamental frequency. The mean dominant frequency of the last pulse had a lower value relative to the first pulse. Most energy of the calls was distributed below 5.0 kHz, as indicated by quartile values. The power spectrum was skewed to the right and had a leptokurtic shape. Calls tend to have high temporal and spectral entropy values. The variables are summarized in Tables I and II and representative calls are shown in Fig. 1.

B. Effects of sex and body mass on acoustic variables

Males and females included in the acoustic analysis did not show significant differences in body mass (Mann–Whitney U-test = 121, $p = 0.110$). Significant differences between sexes were found in the first, second, and third quartiles of the mean power spectrum of the first pulse, call duration, and number of pulses (see supplementary material II¹). All these variables showed higher values in males than in females (Table I). No variable was significantly affected by body mass, and there was no interaction between sex and body mass (see supplementary material II¹).

C. Potential for distinctiveness at the individual level

All acoustic variables showed median PIC values above 1, nevertheless, some variables showed PIC values equal to

TABLE I. Descriptive statistics for acoustic properties of chinchillas' bark calls elicited in a distress context. Column abbreviations: SD, standard deviation; Q1, first quartile; Q3, third quartile. Row abbreviations: DF, dominant frequency; Q25, first quartile of power spectrum; Q50, second quartile of power spectrum; Q75, third quartile of power spectrum; IQR, inter-quartile range of power spectrum; Sk, power spectrum skewness; Ku, power spectrum kurtosis; CD, call duration; PD, pulse duration; PP, pulse period; NP, number of pulses contained in calls; SH, spectral entropy; TH, temporal entropy; H , total entropy. Prefixes F - and L - indicate first and last pulses, respectively. Subindexes b , m , and f indicate beginning, middle, and final part of pulses, respectively.

Variable	All individuals ($N = 27$)		Females ($N = 16$)		Males ($N = 11$)	
	Mean \pm SD	Median (Q1–Q3)	Mean \pm SD	Median (Q1–Q3)	Mean \pm SD	Median (Q1–Q3)
F -DF (Hz)	1259 \pm 721	1115 (684–1477)	1183 \pm 740	1057 (584–1427)	1368 \pm 712	1294 (728–1844)
F -Q25 (Hz)	1401 \pm 462	1454 (1157–1746)	1224 \pm 467	1259 (770–1567)	1659 \pm 323	1708 (1457–1753)
F -Q50 (Hz)	2830 \pm 755	3012 (2417–3374)	2499 \pm 756	2503 (1675–3197)	3310 \pm 442	3359 (2988–3445)
F -Q75 (Hz)	5039 \pm 899	5114 (4583–5793)	4711 \pm 978	4747 (3739–5616)	5516 \pm 494	5309 (5175–5976)
F -IQR (Hz)	3638 \pm 596	3540 (3215–4111)	3488 \pm 623	3288 (3085–4103)	3857 \pm 503	3600 (3529–4108)
F -Sk	5.7 \pm 2.9	5.1 (3.5–6.8)	6.2 \pm 3.1	5.3 (3.6–8)	5.1 \pm 2.5	4.4 (3.5–5.6)
F -Ku	59 \pm 56	40 (20–71)	67 \pm 59	47 (22–88)	48 \pm 50	33 (19–51)
F -SH	0.82 \pm 0.04	0.84 (0.81–0.85)	0.81 \pm 0.04	0.82 (0.78–0.85)	0.84 \pm 0.02	0.84 (0.83–0.85)
F -TH	0.89 \pm 0.02	0.90 (0.88–0.90)	0.90 \pm 0.02	0.9 (0.89–0.91)	0.89 \pm 0.02	0.90 (0.87–0.90)
F - H	0.80 \pm 0.03	0.82 (0.79–0.83)	0.80 \pm 0.04	0.8 (0.77–0.83)	0.82 \pm 0.02	0.82 (0.81–0.83)
F_b -DF (Hz)	1053 \pm 560	873 (632–1409)	1071 \pm 655	800 (570–1504)	1027 \pm 411	995 (710–1262)
F_m -DF (Hz)	1683 \pm 865	1613 (777–2525)	1365 \pm 724	1312 (671–1793)	2146 \pm 871	2482 (1631–2749)
F_f -DF (Hz)	1351 \pm 693	1242 (750–1834)	1272 \pm 699	1141 (732–1638)	1466 \pm 700	1591 (931–1906)
L -DF (Hz)	562 \pm 206	491 (434–604)	532 \pm 153	521 (396–593)	605 \pm 267	483 (471–604)
L -Q25 (Hz)	741 \pm 211	747 (542–839)	735 \pm 220	720 (546–861)	751 \pm 207	774 (587–813)
L -Q50 (Hz)	1696 \pm 473	1564 (1334–1937)	1683 \pm 552	1526 (1323–1878)	1714 \pm 352	1710 (1433–1960)
L -Q75 (Hz)	3601 \pm 776	3488 (3216–3946)	3450 \pm 720	3328 (2994–3922)	3820 \pm 835	3594 (3446–3946)
L -IQR (Hz)	2860 \pm 683	2772 (2447–3042)	2716 \pm 558	2703 (2294–2878)	3069 \pm 815	2877 (2542–3279)
L -Sk	8.2 \pm 2.5	7.8 (6.3–10.1)	8.0 \pm 2.3	7.8 (6.3–9.3)	8.4 \pm 3.0	7.8 (6.5–10.7)
L -Ku	101 \pm 53	92 (63–136)	97 \pm 48	87 (63–118)	106 \pm 61	93 (65–150)
L -SH	0.79 \pm 0.03	0.78 (0.76–0.80)	0.78 \pm 0.04	0.78 (0.75–0.80)	0.78 \pm 0.03	0.78 (0.76–0.80)
L -TH	0.89 \pm 0.03	0.89 (0.88–0.91)	0.89 \pm 0.30	0.89 (0.88–0.91)	0.89 \pm 0.02	0.90 (0.88–0.91)
L - H	0.76 \pm 0.03	0.76 (0.75–0.78)	0.76 \pm 0.03	0.77 (0.74–0.78)	0.76 \pm 0.03	0.76 (0.75–0.78)
L_b -DF (Hz)	520 \pm 161	476 (420–606)	489 \pm 123	489 (380–559)	565 \pm 202	476 (442–630)
L_m -DF (Hz)	612 \pm 252	566 (430–703)	593 \pm 211	595 (394–726)	640 \pm 310	476 (458–671)
L_f -DF (Hz)	453 \pm 147	413 (384–450)	471 \pm 182	413 (378–471)	425 \pm 72	413 (396–423)
CD (s)	3.8 \pm 1.8	3.5 (2.8–4.7)	3.1 \pm 1.6	2.9 (2.0–3.7)	4.8 \pm 1.7	4.7 (4.0–5.1)
NP	8 \pm 4	7 (5–10)	7 \pm 3	7 (4–8)	10 \pm 4	10 (8–11)
F -PD (ms)	165 \pm 44	165 (133–188)	174 \pm 46	170 (158–202)	152 \pm 39	165 (121–175)
F -PP (ms)	552 \pm 107	542 (491–599)	563 \pm 98	547 (510–606)	536 \pm 122	528 (448–585)
L -PD (ms)	170 \pm 68	158 (129–222)	169 \pm 76	149 (121–222)	171 \pm 59	167 (139–214)
L -PP (ms)	540 \pm 99	525 (458–601)	548 \pm 109	527 (459–618)	527 \pm 86	525 (464–565)

TABLE II. Descriptive statistics for the fundamental frequency of chinchillas' bark calls elicited in a distress context. Abbreviations: SD, standard deviation; Q1, first quartile; Q3, third quartile; FF, fundamental frequency; P-one, proportion of individuals having at least one reliable tonal structure in the corresponding temporal position; P-all, proportion of individuals having reliable measures in all corresponding temporal positions; NF-all, number of females having reliable measures in all corresponding temporal positions; NM-all, number of males having reliable measures in all corresponding temporal positions. Prefixes F - and L - indicate first and last pulses, respectively. Subindexes b , m , and f indicate beginning, middle, and final part of pulses, respectively.

Variable	Mean \pm SD	Median (Q1–Q3)	P-one	P-all	NF-all	NM-all
F_b -FF (Hz)	659 \pm 134	669 (534–773)	0.8	0.5	6	4
F_m -FF (Hz)	676 \pm 135	674 (577–792)	0.7	0.4	5	3
F_f -FF (Hz)	575 \pm 104	572 (520–625)	0.7	0.2	2	1
L_b -FF (Hz)	434 \pm 109	416 (361–529)	0.9	0.2	4	1
L_m -FF (Hz)	435 \pm 98	435 (358–506)	0.9	0.2	4	1
L_f -FF (Hz)	358 \pm 63	348 (310–400)	1.0	0.2	2	2

0.9 in the lower limit of the confidence interval. PIC values were supported by highly significant p -values. The highest median PIC values were for variables from the first pulse: power spectrum skewness, temporal entropy, and dominant frequency at the beginning of the pulse [Fig. 2(a); see supplementary material III¹].

In DFA, the first three functions explain 55% of variance. The first function (DF1) explains 29.6% of variance, being mainly determined by the skewness of the power spectrum of the first pulse (correlated with the kurtosis of the power spectrum of the first pulse) and by the temporal entropy of the first pulse (correlated with the duration of the first pulse). DF2 explains 14.8% of variance, being mainly determined by the number of pulses of the call (correlated with the duration of the entire call), the second quartile of the power spectrum of the first pulse, and the spectral entropy of the first pulse (correlated with the total entropy of the first pulse). DF3 explains 10.7% of variation, being mainly determined by the temporal entropy of the last pulse (correlated with the duration of the last pulse;

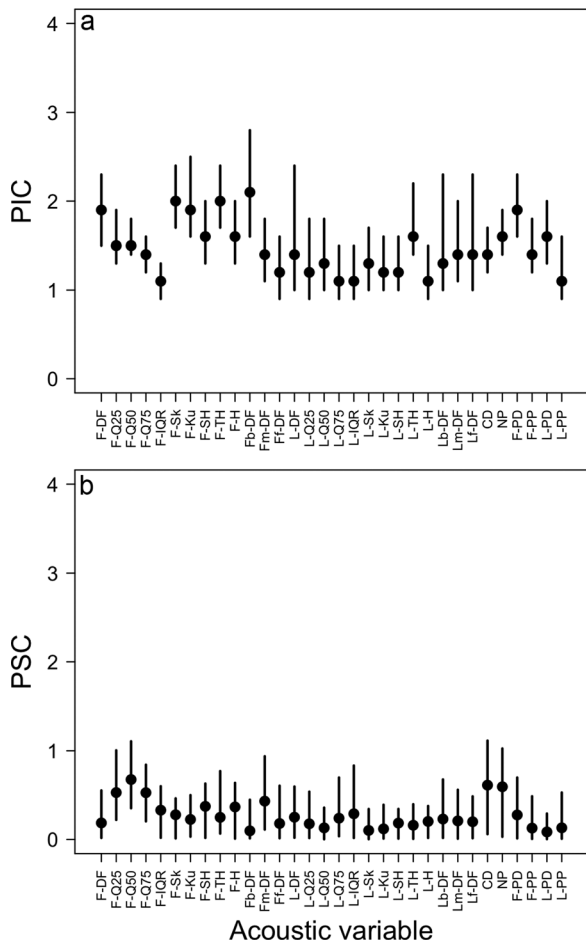


FIG. 2. (a) Variation in PIC of acoustic variables of chinchillas' bark calls elicited in a distress context. (b) Variation in PSC of acoustic variables of chinchillas' bark calls elicited in a distress context. Median and 95% CI in the (a) PIC and (b) PSC for each variable was obtained through a bootstrapped procedure with 1000 iterations. Abbreviations are the same as for Table I.

see supplementary material IV and V¹). Note that highly correlated variables were not included in DFA due to collinearity issues. The graphical representation of call scores obtained in DFA using the individuals as grouping variable is shown in Fig. 3(a). The leave-one-out cross-validation performed under a bootstrapped routine yielded a median of

78.5% [confidence interval (CI) 95%: 70.7%–87.5%] of calls correctly classified for the corresponding individual.

D. Potential for distinctiveness at the sex level

For the PSC, no acoustic variable presented median values above 1. However, the upper limits of the confidence interval at 95% of the PSC reached values equal to 1 in the first and second quartiles of the power spectrum of the first pulse, in the duration of the entire call, and in the number of pulses of the entire call. In these cases, the lower limits of the confidence interval of *p*-values were also significant [Fig. 2(b); see supplementary material VI¹].

In DFA, the most important variables corresponded to the spectral entropy of the last pulse (correlated with the total entropy of the last pulse) and the third quartile of the power spectrum of the last pulse (correlated with the interquartile range of the last pulse; see supplementary material VII and VIII¹). The graphical representation of the call scores obtained in DFA using sex as a grouping factor is shown in Fig. 3(b). Using a leave-one-out cross-validation under a bootstrapped routine a median of 76.9% (CI 95%: 44%–100%) of calls were correctly predicted for the corresponding sex.

IV. DISCUSSION

Our results demonstrate that the variation of acoustic properties measured for chinchillas' bark calls elicited under a distress context is larger between individuals than within individuals. All variables showed median PIC values higher than 1. Although within the confidence interval some variables included values lower than 1, in all cases these were equal to 0.9. In the multivariate analysis, the most important variables contributing to discrimination included spectral and temporal variables, most of them belonging to the first pulse, however, temporal variables from the entire call and temporal variables from the last pulse were also important. The percentage of correct classification of calls obtained in DFA, i.e., 78.5%, having a low confidence interval at 70.7%, suggests a potential for signal distinctiveness among individuals.

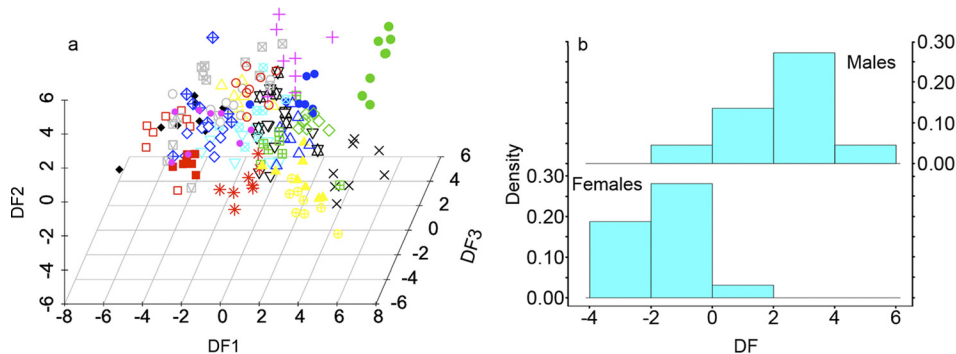


FIG. 3. (Color online) Vocalization scores obtained from DFA based on acoustic properties of the chinchillas' bark calls elicited in a distress context. (a) Discriminant functions 1, 2, and 3 (DF1, DF2, and DF3, respectively) obtained to assess classification of individual calls. Eight random calls obtained from each individual ($N = 27$) are represented by symbols of the same kind. (b) Discriminant function obtained to evaluate classification of calls to the corresponding sex (one call obtained at random from each individual). Histograms show the distribution of vocalization scores obtained for males (upper part) and females (lower part). Note that there is only one discriminant function because the analysis contains only two groups.

Although we found that some variables showed differences between sexes, when analyzing one call per individual all variables showed median PSC values below 1. Nevertheless, almost the same variables that showed significant differences in the linear mixed-effects model analysis showed PSC values equal to or above 1 in the upper limit of the confidence interval, the exception being the third quartile of the first pulse. In the multivariate analysis, the percent of correct call classification in DFA included values below 50% within the confidence interval. These results suggest that the potential for sex distinctiveness of isolated calls is quite limited. Although we measured 32 acoustic variables that were tested statistically, it is possible that other call features not analyzed, e.g., variables from intermediate pulses that were not measured, do help to clearly discriminate isolated bark calls between sexes.

An adaptive explanation for distinctiveness in the bark calls of the animals studied is limited. This is because domestic chinchillas have been artificially selected for peltry and are supposed to descend from 12 wild animals captured around a century ago (Spotorno *et al.*, 2004). Although the evolutionary impact of domestication on chinchillas' acoustic traits is uncertain, wild animals form colonies and individuals are philopatric. Distinctiveness allows associative learning (Owren and Rendall, 2001) and therefore may help to recognize kin, to discriminate less reliable individuals that produce false alarms, and to improve the determination of the level of danger when several individuals call simultaneously (Blumstein *et al.*, 2004; Blumstein and Munos, 2005; Pollard, 2011).

The results of our analysis are in partial agreement with the study of Matrosova *et al.* (2011) on alarm calls of captured individuals of three different mammals species, i.e., speckled ground squirrel (*S. suslicus*), yellow ground squirrel (*Spermophilus fulvus*), and yellow-billed marmot (*M. flaviventris*). They found that spectral and temporal variables of calls associated to this stressful situation could provide cues about the identity of individuals, but a minor group of variables provide sex distinctiveness in *M. flaviventris* and *S. fulvus*, and none in *S. suslicus*. Among these species, differences regarding sexual distinctiveness seem to be concordant with the degree of sociality (Matrosova *et al.*, 2011).

In our study, no clear explanation for the lack of sexual distinctiveness observed can be offered, because in domesticated animals breeding and other social behaviors are expressed under human intervention. Nevertheless, with an increased sample size and a wider range of body mass, an effect of sex may be identified. A potential benefit of sexual distinctiveness may be associated to differential behavioral responses according to the sex of the emitter (e.g., Aubin *et al.*, 2007). In addition, it may help to improve the recognition between individuals of monogamous pairs (Grau, 1993). Future studies should evaluate the occurrence of distinctiveness at the sex level in wild animals. Other examples of spectral and temporal variables contributing to individual distinctiveness correspond to the gray mouse lemur (*M. murinus*; Leliveld *et al.*, 2011) and the baboon (*Papio cynocephalus ursinus*; Fischer *et al.*, 2002); this last species also showed differences between sexes.

A common trend in acoustic signals of different vertebrates is the inverse relationship between body mass and fundamental frequency (e.g., Ryan and Brenowitz, 1985; Bennet-Clarck, 1998). Although the limited number of calls with reliable tonal structure in our sample precluded performing statistical tests on this variable, we found that spectral variables were not significantly affected by the body mass of individuals when comparing vocalizations between sexes. Therefore, our results are not in agreement with the general predictability of spectral contents by body size. In the koala (*Phascolarctos cinereus*) and the fallow deer (*Dama dama*), not all spectral variables are correlated with body size (Vannoni and McElligott, 2008; Charlton *et al.*, 2011).

We observed that not all individuals produced bark calls under our stimulation protocol. In addition, the occurrence of calls with a reliable tonal structure was variable within individuals. These variations could reflect the arousal and stress level of individuals. For instance, in the yellow-billed marmot (*M. flaviventris*), there is a correlation between the level of faecal glucocorticoid metabolites (hormones secreted under stressful conditions in which measurement give an approximation on the stress level of individuals) and the production of alarm calls (Blumstein *et al.*, 2006), and a negative correlation between the level of glucocorticoids and the production of noisy calls (Blumstein and Chi, 2012). Future studies should evaluate these issues considering an extended sampling period, e.g., several days. This would be of further interest as it may help to elucidate potential mechanisms involved in chinchilla personalities (Carere *et al.*, 2010).

The most common vocalizations produced in stressful situations are the distress calls emitted when animals are captured by predators and the alarm calls emitted when animals detect the presence of predators (Caro, 2005). Our protocol resembled a scenario in which animals are facing the capture by predators. However, we observed that some animals start calling when the experimenter was approaching, i.e., before direct physical contact. According to previous studies, animals can produce another call type characterized by a large and rapid frequency jump, which is produced in situations when an animal feels in extreme danger, which is however rarely produced (Spotorno *et al.*, 2004; Bartl, 2006; Hunyady, 2008). We did not observe this call because in our protocol animals were not stressed to a large extent. In this sense, the bark calls could correspond to some sort of alarm call (Bartl, 2006; Hunyady, 2008). Interestingly, animals reared in artificial conditions may respond to natural threats and react to alarm calls displaying vigilant behavior, as has been shown to occur in individuals of the rodent *Octodon degu* with no previous experience with these kinds of stimuli (Nakano *et al.*, 2013). Given that at least two natural chinchilla predators are known, i.e., culpeo foxes (*P. culpaeus*) and Magellan-horned owls (*B. magellanicus*; reviewed in Spotorno *et al.*, 2004), it would be of interest to determine the behavioral response of captive chinchillas against models of these natural threats.

Regarding auditory capabilities, previous studies revealed that the anatomy of the middle ear and cochlea of chinchillas is similar to that of humans (Daniel *et al.*, 1982;

Bohne *et al.*, 1990), their auditory sensitivity being only one-octave shifted to higher frequencies relative to human sensitivity (Heffner and Heffner, 1991). In addition, frequency and human phoneme discrimination in chinchillas are close to the performance of human listeners (Kuhl and Miller, 1975, 1978; Nelson and Kiester, 1978; Shofner, 2000). Moreover, it is known that chinchillas can detect and discriminate missing fundamental frequencies from harmonic complex tones in a behavioral paradigm (Shofner, 2011; Shofner and Chaney, 2013). By combining this information on the auditory capabilities of chinchillas and the results of our study, we suggest that this rodent has the potential for discriminating among conspecific individuals. It is possible that both individual call distinctiveness and hearing capabilities are associated to the social system of chinchillas. Nevertheless, the occurrence of individual discrimination by signal receivers should be evaluated, since in mammals conspecific individual recognition is variable across species (Blumstein and Daniel, 2004; Schibler and Manser, 2007).

Because domestic chinchillas have been widely used for the study of hearing, including anatomical, behavioral, and neurophysiological studies (e.g., Daniel *et al.*, 1982; Azeredo *et al.*, 1999; Delano *et al.*, 2007; Delano *et al.*, 2008; Elgueda *et al.*, 2011; León *et al.*, 2012), our results indicate that this animal may become an important model for studying auditory–vocal interactions implied in acoustic communication. For instance, in rats it has been found that fear can be transmitted through acoustic signals, but this depends on the integrity of brain auditory structures, and also on the previous experience of individuals (Kim *et al.*, 2010). Therefore, studies on domestic chinchillas may help to elucidate the generality of results which arose from other model species.

Another implication from our results may relate to conservation purposes. Although the existence of call distinctiveness in wild chinchillas should be evaluated, as there could be differences in calls between captive and wild animals (Ouattara, 2009; Nakano *et al.*, 2013), vocalization recordings could be used for future acoustic monitoring plans. This will be valuable as the IUCN catalogues wild chinchillas as critically endangered (D’Elia and Teta, 2008). The advances in technology in non-invasive automated recording devices have allowed implementing acoustic monitoring plans for several species worldwide (Obrist *et al.*, 2010).

Our results suggest that the bark calls of chinchillas elicited in a distress context provide individual distinctiveness, but sexual cues are limited. Further studies are needed to determine if receivers can use these acoustic signatures, allowing conspecific individual discrimination. In addition, the occurrence of distinctiveness in other call types of chinchillas (Bartl, 2006; Hunyady, 2008) should be evaluated. Our results suggest that domestic chinchillas may become important model species for studying auditory–vocal interactions.

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