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ORIGINAL ARTICLE

Sexual dimorphism in the loud calls of Azara's owl monkeys (*Aotus azarae*): evidence of sexual selection?

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Abstract
Primates use different types of vocalizations in a variety of contexts. Some of the most studied types have been the long distance or loud calls. These vocalizations have been associated with mate defense, mate attraction, and resource defense, and it is plausible that sexual selection has played an important role in their evolution. Focusing on identified individuals of known sex and age, we evaluated the sexual dimorphism in a type of loud calls (hoots) in a population of wild owl monkeys (*Aotus azarae*) in Argentina. We found evidence of sexual dimorphism in call structure, with females and males only emitting one type of call, each differing in dominant frequency and Shannon entropy. In addition, both age-related and sex-specific differences in call usage were also apparent in response to the removal of one group member. Future acoustic data will allow us to assess if there are individual characteristics and if the structure of hoot calls presents differences in relation to the social condition of owl monkeys or specific sex responses to variants of hoot calls' traits. This will provide deeper insights into the evolution of vocal mechanisms regulating pair bonding and mate choice strategies in this and other primate species.

Keywords Vocal communication · Loud calls · Dimorphism · Sexual selection · Monogamy · Pair-living

Introduction

Vocal communication has been a central topic of interest for primatologists and evolutionary anthropologists for decades (Seyfarth et al. 1980; Snowdon 1989; Ghazanfar and Hauser 1996; Zuberbühler et al. 1999). The study of this type of communication can lead to insights about the evolution and maintenance of the social systems in which they occur (Mccomb and Semple 2005; Heymann 2003). Among non-human primates, some of the most studied types of vocalizations have been the long distance or loud calls. Loud calls, like chemical signals, are expected to be relatively more important in arboreal species where visibility may limit the value of visual communication (Epple 1974). In primates, these vocalizations have been associated with resource defense (Sekulic 1982; Whitehead 1987; Mitani 1990; Cowlishaw 1996; Steenbeek et al. 1999; Wich and Nunn 2002; Rasoloharijaona et al. 2006), mate attraction (Steenbeek et al. 1999; Wich and Nunn, 2002; Caselli et al. 2018), and infanticide (Wich et al. 2002, 2004). Further, given their important role in maintaining the spatial cohesion of the group, male–female interactions and assisting individuals in the search for potential mates, it is plausible

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that sexual selection has played an important role in their evolution (Delgado 2006).

The formation of a mating pair requires the identification of potential mates, and the ability to differentiate mates from other opposite-sex individuals. Some studies documented variation between the sexes and individual recognition in loud calls in several primate taxa (Benz et al. 1990; Porter 1994; Smith et al. 2009; Rukstalis and French 2005; Terleph et al. 2015). In pair-living and sexually monogamous titi monkeys (*Callicebus* spp.), loud calling is commonly emitted as coordinated duets by pairs. Even when no sex-specific duet contributions have been detected (*C. ornatus*, Robinson 1979; *C. cupreus*, Müller and Anzenberger 2002; *C. nigrifrons*, Caselli et al. 2015), it is possible that sex contributions differ in the acoustic characteristics of syllables that are assembled to compose the song parts of duets' long sequences, allowing individuals to identify the sex of the caller (Caselli et al. 2015).

Another pair-living and sexually monogamous taxon that can serve as a model to examine the possible sex differences of loud vocalizations is *Aotus azarae*, the Azara's owl monkeys of Formosa Province in Argentina. Owl monkeys live in groups composed of a heterosexual pair that mates monogamously (Huck et al. 2014a), one infant, one or two juveniles, and sometimes a subadult (Fernandez-Duque 2016). In the owl monkey population, we study in Guaycolec Ranch, all male and female subadults disperse from their natal groups and become floaters, who range solitarily while looking for a reproductive position in another group (Huck and Fernandez-Duque 2017). Preliminary analyses indicate that, given the relatively low infant and juvenile mortality, there are more floaters than available breeding positions (Huck and Fernandez-Duque 2017), which leads to an intense and frequent competition over breeding positions for both males and females (Fernandez-Duque and Huck 2013). Owl monkeys show extremely low levels of dimorphism in body size, coloration, and the external genitalia, and like other pair-living sexually monogamous taxa, they show an extended form of male care (Huck et al. 2011; Huck and Fernandez-Duque 2012; Spence-Aizenberg et al. 2018a, b).

Based on Trivers' (1972) hypothesis that the sex with less investment in infant care would be the more competitive one, Heymann (2003) proposed that, among New World Monkeys, the degree of male care is related to the influence of sexual selection on the evolution of chemical and vocal communication. He predicted that in taxa where males were the principal providers of infant care, females would vocalize more than males. In contrast to other genera, our knowledge of owl monkey vocal communication that would allow evaluation of the hypothesis remains quite limited. Only two studies on captive animals have assessed the vocal repertoire of *Aotus* (Moynihan 1964; Kantha et al. 2009); in two other studies of vocal communication in wild owl monkeys, the authors were not able to unequivocally identify the sexes or age of the individuals due to the strictly nocturnal habits of the species studied (Wright 1985; Helenbrook et al. 2018). These studies suggested that one call, the hoot call, conveys information over long distances and that could be differentiated into two sub-types, graff and tonal ones (Wright 1985).

The goal of our study was to assess sex differences in hoot calls in wild owl monkeys. Using only information from identified individuals of known age and sex, we first assessed whether hoots are sexually dimorphic, comparing information on the rate of production of graff and tonal hoots. We predicted that tonal and graff hoots would be sex-specific. Second, we compared audio recordings of tonal and graff hoots to test the prediction that there would be acoustic differences in the basic structure of both types of calls. Finally, to examine whether the levels of dimorphism in hoot calls are consistent with the hypothesis proposed by Heymann (2003) we tested the prediction that females would emit more hoot calls than males given the high degree of paternal care in owl monkeys.

Methods

Study area and population

The study area, located in the gallery forests along the Pilagá River in the Argentinean Gran Chaco, is part of the 1500-ha Owl Monkey Reserve established in 2006 (58°13′ W, 26°54′ S). The area includes a mosaic of grasslands, savannas, xeric thorn forests, and semideciduous forests (van der Heide et al. 2012). The climate is subtropical with no marked wet season (1418 mm/year), and extreme low and high temperatures are frequent (daily minimum temperatures < 10 °C between April and September and maximum daily temperatures > 33 °C between September and March; Huck et al. 2017). A system of intersecting transects at 100-m intervals covers approximately 300 ha of forest where all of the data were collected (Fernandez-Duque 2016).

Unlike the strictly nocturnal tropical species of owl monkeys, *Aotus azarae* is unique among the genus because of its cathemeral habits. The Azara's owl monkeys show activity both during the day and night (Fernández-Duque et al. 2010), which allows for detailed behavioral data to be collected from identified individuals during daytime. The relatively small home ranges (mean ± SD: 6.2 ha ± 1.8; Wartmann et al. 2014) make it possible to monitor regularly many focal groups (10–15 groups for behavioral data: Fernandez-Duque 2016).

Data collection

We used data collected through two different procedures (demographic monitoring and captures with physical exams). All data were extracted from the Owl Monkey Project (OMP) relational Access database. For demographic monitoring, every time a group of monkeys or a solitary individual is found, observers enter an “Avistaje” (i.e., a sighting) in the OMP database, where basic demographic data, geolocation, and behaviors noted upon encounter are recorded. We analyzed all avistaje records for which data on hoot calls were available and we analyzed all hoot calls registered during 2001–2017. We analyzed all vocal behaviors entered together with sighting data, not when conducting behavioral focal sampling. To ensure the quality of vocal data, we limited the use of data to those collected by experienced observers, defined as those who stayed in the field at least 4 months and had experience identifying hoot calls. There were 90 sighting records that included information on hoot calls. Fifty-four percent of them ($N=48$) specified the sex of the caller. For all analyses, we classified pair-living adults and floaters as potentially reproductive individuals, and subadults and juveniles still living in their natal groups as non-reproductive ones. We followed Huck et al. (2011) for age classifications of subadults (24.1–48 months) and juveniles (6.1–24 months).

Since 2000, we have conducted 277 captures with physical exams of owl monkeys. In the process, we caught 177 different individuals, whom we physically examined, sampled for biological specimens, and fitted with a bead or radio collar (Fernandez-Duque and Rotundo 2003; Fernandez-Duque et al. 2017). Given the remarkable lack of visible sexual dimorphism (Fernandez-Duque 2011), these procedures have made it possible to reliably identify individuals in the field. Out of 277 captures, we captured potentially reproductive individuals on 191 occasions (69%) and non-reproductive ones on 86 occasions (31%). No hoots were ever registered during captures of non-reproductive individuals. During 29 captures of pair-living adults (15%), there were hoot calls emitted by members of the group left behind.

During six of the captures of pair-living adults we obtained sound recordings of hoot vocalizations produced by the remaining adult in the group while the captured pair mate was being examined. We made the recordings with a Marantz PMD660 Recorder and a Sennheiser ME66 Short Shotgun Capsule Head for K6 Series, at a visually estimated distance of 10–30 m. All recordings were made by two experienced observers (C. Depeine and M. Rotundo). All audio files ($n=111$) were recorded in .wav format, with a sampling rate of 44.1 kHz and 16-bit sound resolution. All recordings were made between 0730 and 1100 h. The material available was obtained from three males and three females (M1 = 6 calls; M2 = 32 calls; M3 = 37 calls; F1 = 8 calls; F2 = 15 calls; F3 = 13 calls).

Acoustic analyses

We performed analyses of the audio files by analyzing calls and syllables separately. To analyze calls, we generated spectrograms of them with a fast-Fourier transform using the Audacity (v. 2.2.1) acoustic software set with a Hanning window and a 2048 points window size (gain = 30 dB, range 40 dB). With a 44.1-kHz sampling rate, each sound sample was 22.7 µs in duration. For acoustic parameter measurements, spectrograms were displayed in the 0–1000 Hz frequency range. The best-quality recordings were retained for call analysis ($n=98$; 88%) and we used sound samples as a unit to accurately measure the parameters call duration, syllable duration, inter-syllabic-intervals, and call rate.

To assess sex differences in the acoustic structure of the hoots, we analyzed 69 bisyllabic calls, 30 from females (F1 = 7 calls; F2 = 11 calls; F3 = 12 calls) and 39 from males (M1 = 2 calls; M2 = 9 calls; M3 = 28 calls). We next analyzed 94 syllables, 42 from females (F1 = 14 syllables; F2 = 6 syllables; F3 = 22 syllables) and 52 from males (M1 = 4 syllables; M2 = 12 syllables; M3 = 36 syllables). The syllables extracted from each call were labeled according to their position (1 or 2) in the call. To ensure that the loudest peak in each file was the same, all sound files were rectified for DC-offset and normalized using SoundExchange (SoX, v. 14.4.1). Individual syllables were exported in .wav format for subsequent analysis with the seewave Package, v. 2.0.5 (Sueur et al. 2008). Many recordings (22/69 = 32%) were contaminated by low-frequency (< 100 Hz) sounds due to equipment handling and/or high-frequency (> 800 Hz) sounds, mainly from insects and birds, that overlapped with the signal of interest. Therefore, using the ‘ffilter’ function of the seewave package, syllables were band-filtered between 100 and 800 Hz where most of the syllable sound energy was concentrated. Subsequent visual inspection of the spectrograms ensured that the signal of interest was devoid of any obvious sound contamination.

To quantify the degree of syllable noisiness, we measured the Shannon spectral entropy using the ‘sh’ function of the seewave package. On a scale from 0 to 1, noisy sounds have high entropy compared to purer sounds. To determine the dominant frequency of the signal, we generated a power spectrum of each syllable using the seewave function ‘spec’ and we elected a window length of 4096 points to increase the frequency resolution (10.8 Hz). Using the ‘fpeaks’ function of the seewave package, we then searched for the ten largest peaks of the frequency spectrum. The largest peak of each spectrum was retained as the dominant frequency. In females, the dominant frequency of multisyllabic calls may go up or down and the change is quite noticeable when listening to the audio files. To determine whether there was a consistent pattern in frequency change, we tracked the pitch of 36 tonal hoot syllables using the Praat software (v. 6.0.52). To improve pitch accuracy, such analysis was done after reducing the background noise on the spectrogram using the 'noise reduction' function in Audacity. Tracking the pitch of graff hoot syllables, on the other hand, was not possible due to their noisy content with many tightly packed bands of modulated sound energy covering a broader frequency spectrum.

We automatized all measurements of spectral entropy, syllable duration, and dominant frequency together with syllable filtering and graphic displays of frequency spectra with a script written in the R environment (v.3.3.3) (R Core Team 2008).

Statistical analyses

In considering the data obtained through demographic monitoring, we used a χ^2 test to estimate the probability of obtaining the observed difference in the frequencies of tonal and graff hoots emitted by females and males, or a more extreme one, assuming equal proportions for both sexes as the null model. Additionally, to evaluate the prediction that hoot calls would be female-biased, we used a χ^2 test to estimate the probability of obtaining the observed difference in the frequencies of loud calls given by females and males, or a more extreme one, given the null model.

All statistical analyses were performed in R version 3.6.0. (R Core Team 2019). We used a linear mixed model using R package lme4 (v. 1.1-21; Bates et al. 2015) to evaluate how well sex predicts the variation of each parameter mentioned above. Due to the extent of non-independence of calls, we included the identity of the monkeys as a random factor while sex was fitted as a fixed factor.

For syllable analyses we used a linear mixed model to evaluate how well sex and, in this case, the position of syllables in call sequence (syllable one or two) explain the variation on each parameter. We included the identity of the individuals as a random factor and sex and syllable's position as fixed ones. To determine the statistical significance of the models, we only compared nested models, varying only in one factor in each comparison. Since random effects were the same in each model, we used the "anova" function (likelihood ratio test) of 'stats' package version 3.7.0 in all comparisons.

To estimate the probability of obtaining the observed difference, or a more extreme one, in the pitch of female hoot syllable we performed a Wilcoxon test for paired samples. The significant level was set to 5% in all analyses and the data are presented as mean ± SD. We also report confidence intervals since they are more informative than *p* values alone (Wasserstein and Lazar 2016; Nakagawa and Cuthill 2007; Ziliak and McCloskey 2008). We tested the assumptions of the linear mixed model using visual diagnostic plots for the residuals. None of our parameters violated the assumptions of normality or homogeneity of variance of the residuals.

Ethical note

We have captured individuals regularly since 2000 using an injection rifle and disposable darts loaded with 0.5 ml of ketamine hydrochloride. Since then, we have evaluated the potential effects of capture on animal welfare and on population structure (Juarez et al. 2011; Fernandez-Duque et al. 2017).

We fitted all individuals with a radio or a bead collar (Fernandez-Duque and Rotundo 2003; Juarez et al. 2011; Fernandez-Duque et al. 2017), depending on the age of the monkey and our interest in being able to locate it reliably. The radio collar has consisted of a transmitter package mounted on a ball-chain collar with a 15-cm whip antenna.

All procedures conformed to Argentinean laws and were approved at different times by the National Wildlife Directorate in Argentina and by the animal research committees of the Zoological Society of San Diego (2000–2005), the University of Pennsylvania (2006–2011), and Yale University (2012–2018). All animal procedures followed the guidelines for the treatment of animals for teaching and research recommended by the Animal Behaviour Society (2014).

Results

Owl monkeys produced two perceptually distinct types of hoot calls (see Online Resources 1 and 2 for an audio of tonal and graff hoots). Tonal hoot calls exhibit a narrowband tonal structure with occasional harmonics whereas graff hoot calls are essentially noisy and broadband, with sound energy appearing fuzzier on the spectrogram (Fig. 1). Each type of vocalization can be emitted as a single syllable or as a sequence of two or three similar ones (multisyllabic calls). Here, a syllable is defined as a continuous trace on the spectrogram (Fig. 2).

Further, males and females emitted different types of vocalizations. No graff hoots were registered from females, nor were any tonal hoots registered from males. When examining demographic monitoring data, of all records of vocalizations from identified males ($N=16$), 88% were graff hoots and 12% were only classified as "hoot" without specifying which type. On the other hand, for all records of vocalizations from identified females ($N=32$), 85% were tonal hoots and 15% were vocalizations only described as "hoots". Females called more often than males (female, $N=32$; male, $N=16$ hoots; Chi-square test for given probabilities, $\chi^2=5.33$, $df=1$, $p=0.02$).

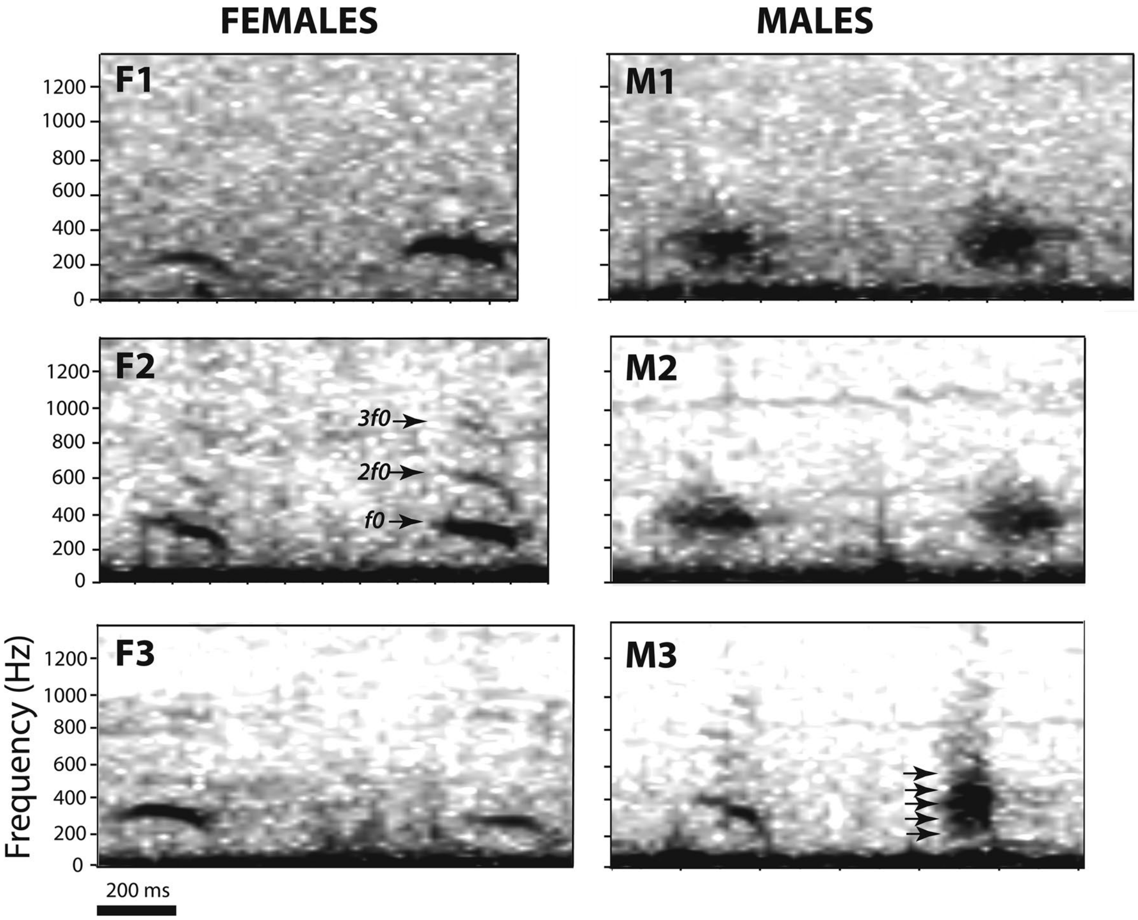

Fig. 1 Exemplars of *Aotus* hoot calls for three females and three males. Two variants are shown: A tonal hoot from female 2 (F2) showing the presumptive fundamental sound (f0) with two overlaid harmonics (2f0 and 3f0). A graff hoot from male 3 (M3) in which the first syllable is less noisy (lower entropy) compared with the second syllable. The latter displays many bands of sound energy between 200 and 600 Hz (*arrows*). Note the change in the pitch of the female hoot calls between first and second syllable: the pitch increases (F1), remains stable (F2), or decreases (F3)

Likewise, the capturing of males or females elicited very different responses from the animals left behind. When we captured the adult female in the group, only graff hoots were produced by a remaining member of the group ($N = 16$ captures). On 14 of the 16 captures ($N = 12$ different pairs), it was the adult male who produced graff hoots. On the other hand, when we captured the adult male in the group, only tonal hoots were emitted by a remaining member of the group ($N = 10$ captures). In eight of the ten captures ($N = 7$ different pairs), it was the adult female who emitted the tonal hoots. As noted, in four captures we could not determine the sex or age of the producer of the calls, however, we never heard a tonal hoot during the capture of an adult female or a graff hoot during the capture of a male. Furthermore, we have never registered any hoot, graff, or tonal emitted by a remaining member of the group during 86 captures of non-reproductive individuals (Chi-square test of independence: $\chi^2 = 112.73$, $df = 1$, $p < 0.001$).

Calls of males were, on average, shorter than those of females (879 ± 122 vs. 981 ± 149 ms, respectively). Further, the intersyllable intervals of males were, on average, shorter than those of females (503 ± 105 vs. 527 ± 125 ms, respectively). The models assessing how well sex of the caller explains duration and intersyllable intervals did not reach statistical significance (Table 1).

When analyzing sex differences in the parameters extracted from syllables, no model reached statistical significance for explaining statistical variability of duration by the sex of the caller or the position of the syllable. On the other hand, the models did reach statistical significance for explaining variability of entropy and dominant frequency by sex and syllable position (Table 2). Specifically, the entropy was higher in male than female calls and was higher on the first syllable of the hoots analyzed (Table 3). The percentage of variance explained (R^2) by the fixed effects of the model was 48% while the percentage

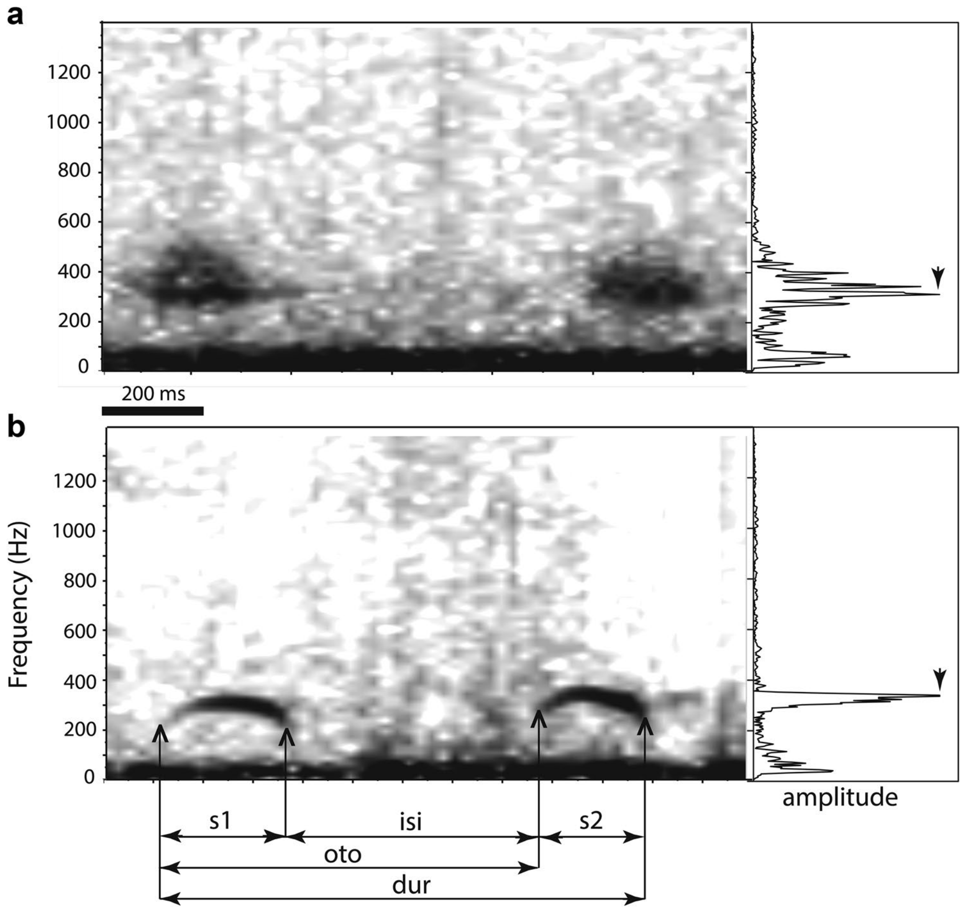

Fig. 2 Spectrograms of Azara's owl monkeys loud calls: **a** graff hoot from male 2 and **b** tonal hoot from female 1. The temporal acoustic parameters measured in this study are shown at the bottom. For each type of call, a power spectrum of the second syllable is shown at right. The *vertical arrowhead* points to the syllable dominant frequency (see text for more details). *dur* call duration, *s1* duration of syllable 1, *s2* duration of syllable 2, *isi* intersyllable interval, *oto* onset-to-onset time interval

Table 1 Result of model comparisons among models including single fixed effects (sex) and the null model

Dependent variable	Model	χ^2	*df*	*p*
Duration (ms)	Model 1 (sex), null	0.25	1	0.62
Intersyllable interval (ms)	Model 1 (sex), null	0.02	1	0.88

of variance explained by the random effects (individual) was 8%.

Similarly, the dominant frequency was higher in male calls, and the second syllable of hoots showed higher values of the variable (Table 3, Fig. 3). In this case, the random effects did not explain any variance of the response

Table 2 Result of model comparisons among complete models (including the interaction among predictor variables sex and syllable), models including simple fixed effects (sex and syllable) and models including single fixed effect

Dependent variable	Model	χ^2	*df*	*p*
Duration (ms)	Complete model (Sex × Syl), model 1 (Sex + Syl)	0.84	1	0.34
	Model 1 (Sex + Syl), model 2 (Sex)	0.16	1	0.7
	Model 2 (Sex), null	0.09	1	0.8
Entropy (Hz)	Complete model (Sex × Syl), model 1 (Sex + Syl)	0.44	1	0.5
	Model 1 (Sex + Syl), model 2 (Sex)	6.05	1	0.01
	Model 1 (Sex + Syl), model 3 (Syl)	11.71	1	< 0.01
Dominant freq (Hz)	Complete model (Sex × Syl), model 1 (Sex + Syl)	0.21	1	0.6
	Model 1 (Sex + Syl), model 2 (Sex)	5.3	1	0.02
	Model 1 (Sex + Syl), model 3 (Syl)	14.1	1	< 0.01

When models with only one fixed variable did not account for enough variance to reject the null hypothesis at the specified significance level, we compared the simplest model with the null one variable, suggesting no inter-individual variability on dominant frequencies. The fixed effect explained the 28% of model's variance.

Table 3 Sex differences in the mean, SD, and confident intervals (95%) of the statistically significant variables (entropy and dominant frequency) extracted from syllable analyses

Variable	Mean	SD	Confidence interval (95%)	
			Lower	Upper
Entropy				
Females	0.47	0.04	0.46	0.48
Males	0.52	0.02	0.51	0.52
Syllable 1	0.50	0.03	0.49	0.51
Syllable 2	0.49	0.04	0.48	0.50
Dominant frequency				
Females	0.31	0.03	0.30	0.32
Males	0.34	0.03	0.33	0.35
Syllable 1	0.32	0.03	0.31	0.33
Syllable 2	0.33	0.03	0.32	0.34

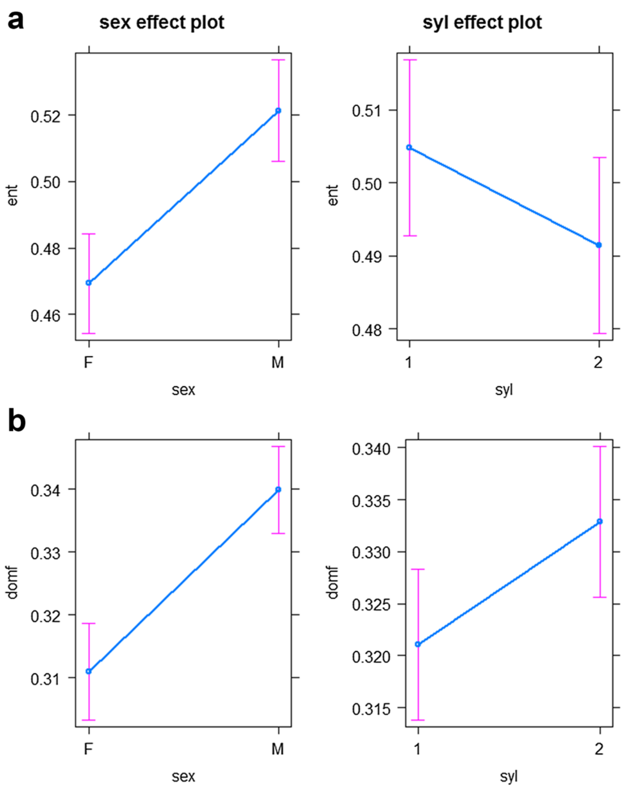

Fig. 3 Effect plot of entropy (**a**) and dominant frequency (**b**). On both graphics, sex differences (F = females and M = males) are shown on the left while syllable differences (1 = first syllable of the calls and 2 = second syllable of the calls) are shown on the right

The pitch of 36 tonal hoot syllables analyzed did not show statistical differences between syllables in any female (Table 4, Fig. 4).

Discussion

Our study of Azara's owl monkeys provides evidence of sex differences in vocal communication, specifically in loud calls. Detailed registers from identified individuals indicated that females only emit tonal and males only emit graff hoots. Our data also showed that male calls had higher entropy and dominant frequencies and these parameters also varied depending on the syllable position (one or two). Further, sex and syllable position explained more of the variation of entropy than the variation of dominant frequency.

The quantitative analyses of owl monkey hoots indicate that there are sex-related differences in their calls. Given the fact that owl monkeys from Argentina do not exhibit any striking morphological/anatomical differences between sexes (Fernandez-Duque 2011), it is likely that such differences arise from allometric traits driven by factors other than body size or body weight (Garcia et al. 2017). In the past, it has been proposed that sexual selection may have played a role in the evolution of sexual dimorphism in loud calls (Delgado 2006; Snowdon 2017). The sexual dimorphism we found in *Aotus* calls has been proposed for other non-sexually dimorphic primate taxa as in indris (*Indri indi*, Gamba et al. 2016), golden lion tamarins (*Leontopithecus rosalia*, Benz et al. 1990), common marmosets (*Callithrix jacchus*, Norcross and Newman 1993), and Wied's black-tufted-ear marmosets (*Callithrix kuhlii*, Smith et al. 2009). A possible explanation could be that differences in male and female calls allow other individuals to identify the sex of the caller; however, a more definite evaluation of this hypothesis requires an approach that includes certain manipulation of conditions, like playback experiments. From early on in the Owl Monkey Project, we have relied on playing back hoot calls to assess presence/absence of owl monkeys in remote areas and to find groups and floaters for capturing them. In the beginning, we did not have an adequate understanding

Table 4 The pitch value (mean ± SD) of female hoot syllables is shown according to syllable position (S1 vs. S2) within the call

Female	*n*	S1	S2	V	*p* value
F1	6	292.40 ± 14.44 Hz	314.02 ± 31.00 Hz	2	0.0938
F2	6	309.52 ± 31.76 Hz	292.19 ± 9.54 Hz	16	0.3125
F3	6	300.23 ± 9.67 Hz	295.90 ± 22.61 Hz	28	1.0000

The *p* values associated with the paired samples Wilcoxon statistics (V) are reported separately for each female

n number of calls

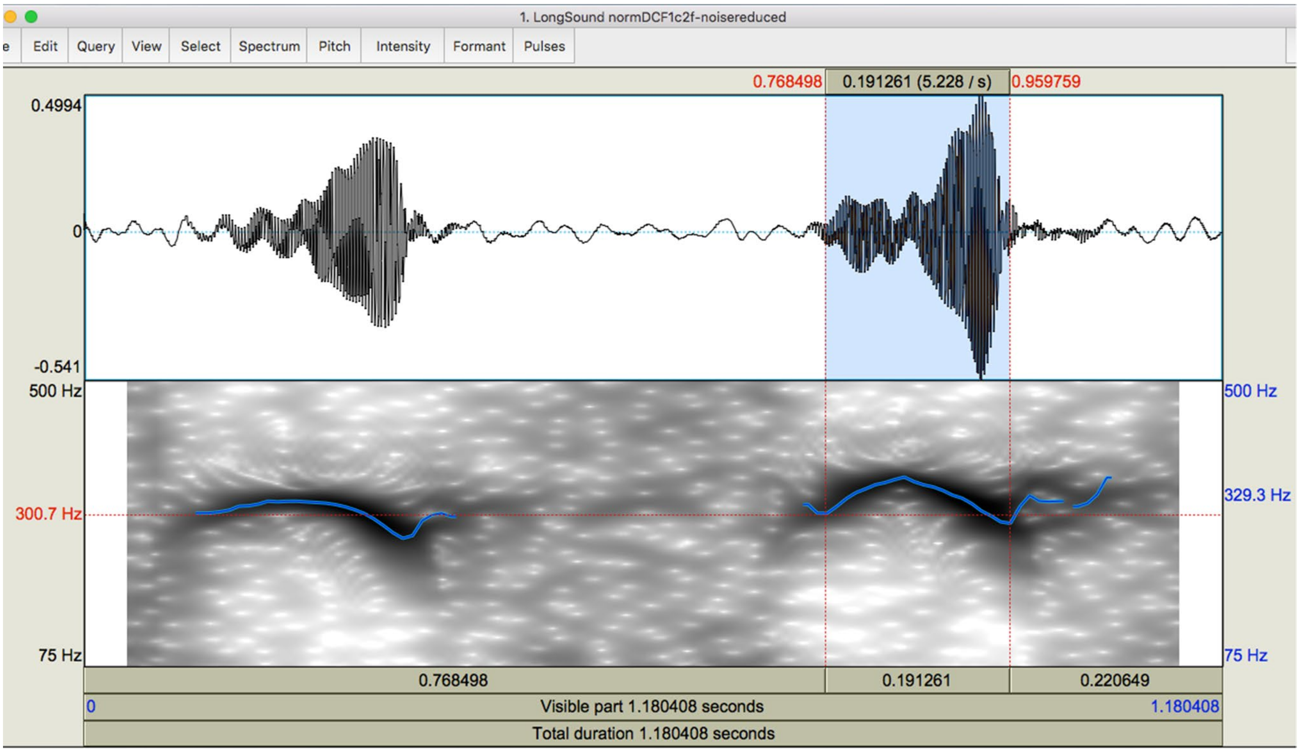

Fig. 4 Pitch analysis of a hoot call (female 1, call 2). The *top panel* of the Praat software window shows the amplitude modulation of the call. The *bottom panel* shows the spectrogram, which displays both frequency values (*in red*) and pitch values (*in blue*). After background noise reduction, the blue line falls exactly on the presumptive fundamental of S1 and S2, respectively. The *two vertical red lines* denote the time interval selected to collect a vector of pitch values, which was saved as a text file

of their vocal communication. So, it was only retrospectively that we realized that the playing back of graff hoots was more effective in attracting individuals and usually led to the capture of females. Further, preliminary results from systematic ongoing playback experiments led by one of us (AGC) have shown that male and female pairs reacted differently to graff and tonal hoots recordings, with both sexes showing an increase of socio-sexual behaviors toward their partners when a simulated same sex competitor was played back (García de la Chica, unpublished). Although beyond the scope of this study, these preliminary findings suggest that some acoustic parameters in owl monkey hoot calls allow individuals for identification of the sex of the caller.

It follows that our data seem to support the hypothesis proposed by Heymann (2003) that in taxa where males are the principal providers of infant care, loud calls would be female-biased. Given that in monogamous species, sexual selection may apply equally to both sexes, and that in owl monkeys, males are heavily involved in energetically costly parental care activities (Rotundo et al. 2005; Huck and Fernandez-Duque 2012) it may be that females face greater intrasexual competition to choose the best male. Our data suggested a female-biased pattern in loud calls with females vocalizing up to twice as much as males. This female-biased pattern in the production of loud calls show contradictory results in the literature. While in captive common marmosets (*Callithrix jacchus*) and golden lion tamarins (*Leontopithecus rosalia*) males and females showed similar rates of loud calls (McLanahan and Green 1977; Norcross and Newman 1993), results from captive *Saguinus oedipus* showed adult females emitting almost three times more loud calls than males (McConnell and Snowdon 1986).

Unlike the cooperative breeding social systems usually observed in callitrichid primates, *Aotus* groups do not contain “helpers” and infant care is provided exclusively by the adults in the group (Rotundo et al. 2002; Huck and Fernandez-Duque 2012). Infants are transported by the adult male 84% of the time after the infant’s first week of life (Rotundo et al. 2005); even during the exceptional cases of twin births, which could entail a double effort of transporting the infants, the mothers did not carry them more frequently than mothers of singletons (Huck et al. 2014b). These observations, even from relatively infrequent events, may be indicating that there are selective pressures against *Aotus* females to increase the amount of infant care.

Our findings notwithstanding, like for most of field primatology data ever collected, one must be cautious and consider other factors that may be influencing observational data. First, with only six individuals included in our acoustical analyses the sample size is small, and the contribution of each individual on the analyses is not the same, with a big variability especially for males. Thus, even when this variability should be partially controlled by the design of our statistical models, our results must be interpreted with caution and data from more identified individuals are undoubtedly needed for further comparisons. Further, we cannot rule out the influence of potential observer bias in noting and recognizing tonal hoots more frequently than graff ones or the fact that it is impossible to have a true systematic random sampling design. To address the latter issue, we are currently implementing the use of passive terrestrial acoustic recorders, which allow true systematic recording across the 24 h. Unfortunately, we still do not know if loud calls encode signals about pair membership, which could inform other individuals about the social condition of callers without the necessity of direct, costly fighting. More acoustic data on identified pairs and solitary individuals will show if the structure of hoot calls present differences in relation to the social condition of owl monkeys, which will provide us deeper insights into the evolution of vocal mechanism regulating pair bonding and mate choice strategies in this species.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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