The effects of unrelated offspring whistle calls on capybaras (*Hydrochoerus hydrochaeris*)

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Abstract

Parent-offspring vocal communication, such as the isolation call, is one of the essential adaptations in mammals that adjust parental responsiveness. Thus, our aim was to test the hypothesis that the function of the capybara infants' whistle is to attract conspecifics. We designed a playback experiment to investigate the reaction of 20 adult capybaras (seven males and 13 females) to pups' whistle calls – recorded from unrelated offspring – or to bird song, as control. The adult capybaras promptly responded to playback of unrelated pup whistles, while ignoring the bird vocalisation. The adult capybaras took, on average, 2.6 ± 2.5 seconds (s) to show a response to the whistles, with no differences between males and females. However, females look longer (17.0 ± 12.9 s) than males (3.0 ± 7.2 s) toward the sound source when playing the pups' whistle playback. The females also tended to approach the playback source, while males showed just a momentary interruption of ongoing behaviour (feeding). Our results suggest that capybara pups' whistles function as the isolation call in this species, but gender influences the intensity of the response.

Keywords: animal communication, bioacoustics, Caviomorph, parent-offspring communication, vocal communication.

Os efeitos do chamado de assobio de filhotes não aparentados em capivaras (*Hydrochoerus hydrochaeris*)

Resumo

A comunicação vocal entre pais-filhotes, tal como os chamados de isolamento, é uma das adaptações essenciais nos mamíferos para o ajuste da resposta parental. Assim, nosso objetivo foi testar a hipótese de que a função do chamado de assobio em filhotes de capivara é para atrair co-especificos. Delineamos um experimento via playback para investigar a reação de 20 capivaras adultas (sete machos e 13 fêmeas) ao chamado de assobio de filhotes não aparentados e como controle usamos o chamado de um pássaro. As capivaras adultas prontamente responderam ao playback de assobios de filhotes não aparentados, enquanto ignoraram as vocalizações de pássaro. As capivaras levaram, em media $2,6 \pm 2,5$ segundos (s) para mostrar a resposta para os assobios, não havendo diferença entre machos e fêmeas. No entanto, fêmeas permanecem mais tempo ($17,0 \pm 12,9$ s) do que os machos ($3,0 \pm 7,2$ s) para retornar da fonte sonora após o playback de assobio iniciar. As fêmeas também tendem a aproximar-se da fonte sonora, enquanto os machos fazem uma breve interrupção do comportamento que estão engajados (comendo). Os resultados sugerem que a função do chamado de assobio de filhotes de capivaras é um chamado de isolamento na espécie e que o gênero influencia a intensidade da resposta.

Palavras-chave: comunicação animal, bioacústica, Caviomorfos, comunicação parente-filhote, vocalização.

1. Introduction

Parent-offspring vocal communication is one of various essential mammalian adaptations to adjust parental reaction, discrimination, recognition, and consequent care of infants (Sèbe et al., 2007). Many examples have showed that infant mammals evolved signals to maintain maternal responsiveness (Gonzalez-Mariscal and Rosenblatt,

1996; Charrier et al., 2002), to alert parents about pup separation (Kober et al., 2007) or imminent attacks by predators or conspecifics (Blumstein and Daniel, 2004). Based on the evidence that common neural structures and neurochemical systems in different mammals underlie the production and perception of these vocalisations, Newman

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(2007) proposes their inclusion in a functional category called 'crying', common to all mammalian infants and the adults of some species. The proposed function of these calls is the re-establishment of contact between mother/caretaker and infant. An inference arising from this proposed function is that mothers should be able to discriminate their own offspring's isolation calls from those of unrelated pups and respond preferentially to them, thus diminishing the costs of misdirected care and increasing their own infant's chances of survival. In support of this proposition females from different species were found to show this ability (reindeer: Espmark, 1971; primate infants: Newman, 2004; murine rodents: Sales and Smith, 1980; caviomorph rodents: Eisenberg, 1974 (*Octodon degus*); Berryman, 1976; Coulon, 1982; Monticelli et al., 2004; Tokumaru et al., 2006 (*Cavia porcellus*).

Nonetheless, a lack of discrimination between related and unrelated offspring calls associated with a generalised response was also found in some species (Weary et al., 1996; McCulloch et al., 1999; Tokumaru et al., 2006; Kober et al., 2007; Bohn et al., 2009). For example, in gray seals the mothers' ability to discriminate the calls was recorded in two populations, with and without the presence of allosuckling (McCulloch and Boness, 2000). In pigs, sows showed a slightly stronger response to their own pups but also responded to unrelated pups (Illmann et al., 2002).

The hypothesis for response to unrelated offspring could be linked to the lack of differences between individual calls (vocal signature), which makes it difficult to discriminate the calls. However, a lack of vocal signature was not the case with guinea-pigs (Tokumaru et al., 2004), gray seals (McCulloch et al., 1999), and great spear-nosed bats (Bohn et al., 2009). Acoustic analyses of pups' isolation calls in these species showed that they were individually distinctive. Conversely, Boness (1990) suggested that the low reproductive costs of fostering in Hawaiian monk seals (*Monachus schauinslandi*) could explain the lack of maternal discrimination between related and unrelated pups' vocalizations. Bohn et al. (2009) proposed that great spear-nosed bat (*Phyllostomus hastatus*) females' response to in-group but unrelated pups' calls can be adaptive, if one considers the species' social structure. Unrelated reproductive females roost together in stable long-term social groups, forage together and give birth synchronously. Non-volant pups occasionally fall from the cave ceiling and can be attacked by females from other groups. In-group females respond to the isolation calls of fallen pups and, although they do not usually retrieve them, their presence protects pups from being captured by out-group females. The authors propose that in such a stable social structure this alloparental care can represent long-term cooperation among reproductive in-group females, and this also seems likely for capybara social groups.

Capybaras (*Hydrochoerus hydrochaeris*) are the largest extant rodents. They live in long-lasting and territorial groups composed of dominant male and females – which are probably kin – infants, young and one or more subordinate males (Ojasti, 1973; Azcárate, 1980; Macdonald et al., 2007).

The females are particularly cohesive, tend to give birth synchronously, and show alloparental behaviour, probably because they are closely related kin (Ojasti, 1973; Azcárate, 1980; Macdonald, 1981; Herrera and Macdonald, 1993; Eisenberg and Redford, 1999; Nogueira et al., 2000). The males do not usually provide parental care, but are tolerant to the presence of the young (Ojasti, 1973; Azcárate, 1980).

Capybara infants are precocious, fully mobile from birth, and can occasionally lose contact with the group when grazing or travelling (Herrera and Macdonald, 1993). Isolated infants emit loud, repetitive, whistle calls (Barros et al. 2011; Figure 1a). Non-systematic observations of responses to these calls have been reported in the form of adults moving closer to the calling infant (Ojasti, 1973; Azcárate, 1980; Lord, 1994; Yáber and Herrera, 1994; Murphey et al., 1985; Barros et al., 2011). The animals that responded were not identified in these observations, which make it difficult to draw conclusions about their social relationships. Hunters in Brazil have traditionally taken advantage of the responses to these vocalisations; they use wood or metal whistles that sound like the infants' calls to attract adult capybaras (Nogueira-Filho, personal observation). These instruments can be found in a number of shops that cater to hunters and animal watchers.

The contexts for whistle emission and the observations that adults respond to them indicate that these calls may function to attract conspecifics to the isolated infant. Thus, our aim in this work was to test the hypothesis that the function of the infants' whistle is to attract conspecifics. Since parental care (infant reunion, predator watching and allosuckling) is provided by all females in a capybara group, (Ojasti, 1973; Macdonald, 1981; Nogueira et al., 2000), probably because they are closely related kin, we predicted that the females would respond indiscriminately regardless of parent-offspring relationship. Additionally, we predicted that the females would be more responsive to the infants' isolation calls than the males, as the latter do not play a part in specific infant care (Ojasti, 1973).

2. Material and Methods

2.1. Housing and animals

The experiment was conducted at the Laboratório de Etologia Aplicada (LABET), Universidade Estadual de Santa Cruz, Ilhéus, Bahia, Brazil (14° 47' 20" S, 39° 02' 56" W). On this site, three herds of capybaras were kept in three paddocks (1,000m², 5,600m² and 3,000m², respectively). Each paddock had a water tank of 30m² and two of them were crossed by a natural stream. Vegetation included several species of shrubs and trees. Inside each paddock an area of 30m² (10.0x3.0x1.8m) was delimited by a wire fence and used as a test arena (Figure 2).

Experimental animals were seven adult males and 13 adult females from the three different capybara groups. Sixteen of the animals were born in different captivity centres and brought to LABET four years before this study. The other four animals (one female and three males) were born at LABET. All females had given birth at least once,
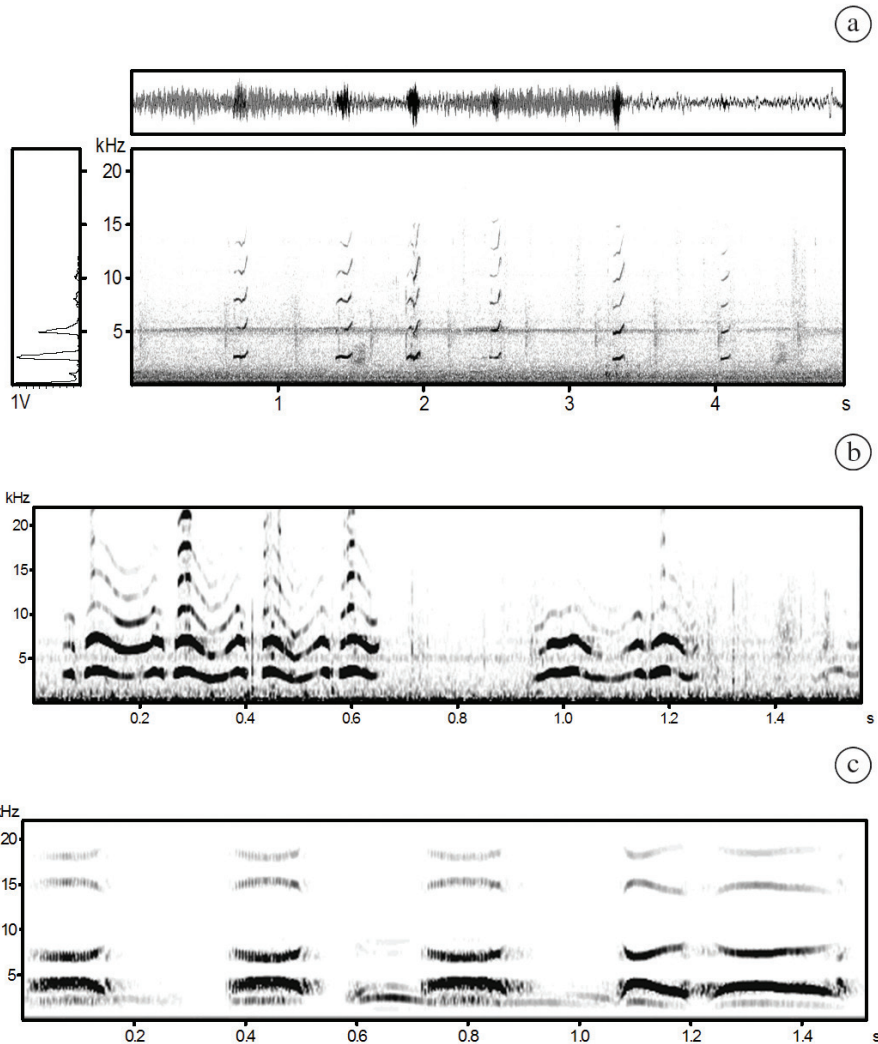
Figure 1. The first spectrogram (a) shows a bout of capybara pups' whistles; the spectrograms of (b) whistle call and (c) birdsong playback, treatment and control, respectively, represent the stimulus of calls released for male and female adult capybaras.
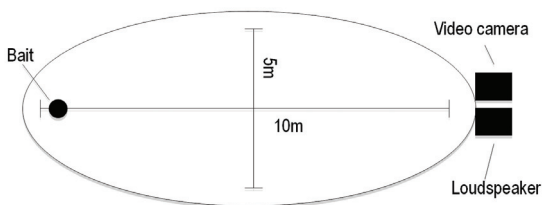

Figure 2. Diagram representing the test arena experimental area and the equipment location.

except the one born at LABET, which was nulliparous. None was lactating at the time of the experiment. All individuals were identified with ear tags.

Capybaras were fed daily at around 17h00. The diet included Napier grass (*Pennisetum purpureum)*, corn grain, soybean meal and mineral salt (Riocon®, Bahia, Brazil 15g per animal). Water was available *ad libitum*.

2.2. Recordings of pups' vocalizations

We recorded the pups' whistle playback (experimental stimuli) from three capybara pups that were unrelated and unfamiliar to the experimental subjects. The pups, about 25 days old (2.5 kg), were found wandering alone near the Cachoeira River in Itabuna, state of Bahia, Brazil, and brought to LABET by members of the Brazilian environmental agency (IBAMA). They were kept together in a cage isolated from other capybaras. They emitted whistles spontaneously, without any manipulation. These emissions were recorded and used as experimental stimuli. To record vocalisations, we used a Sennheiser ME 66/ K6 (Sennheiser Corp., Old Lyme, CT, USA) directional microphone (0.02 – 20 kHz ± 1.0 dB) connected to a Marantz (D&M Professional, Kanagawa, Japan) PMD 670 solid state recorder (0.02 – 20 kHz ± 0.5 dB). During the recordings the microphone was located at 0.5 to 1m

away from the pups. All recordings were sampled at 16 bit and 48 kHz. The sound files were saved in WAV format and stored in compact discs. As a neutral control sound, we recorded calls emitted by *Pitangus sulphuratus*, a common bird in the study site.

2.3. Playback stimuli

The sound files in WAV format were transferred to a laptop (Compaq Computer Corporation, Texas, USA). We used the software Avisoft-SASlab Pro (Avisoft Bioacoustics, Berlin, Germany) to select the calls with the best background signal-to-noise ratio. Then the software Audacity 1.3 (General Public License) was used to edit the sound stimuli. To build the whistle playback (WP) we selected whistle calls with a bout of 1.5s, from one out of the three abandoned pups (Figure 1b). These calls were selected for the sound quality (without interference). The calls were repeated five times, alternating with four silent intervals of 5s. Thus the WP lasted 27.5s, which mimics the natural duration of the bouts (Barros, 2009). The same procedure was adopted to prepare 27.5s of control stimuli playback (CP) with *Pitangus sulphuratus* calls (Figure 1c). After editing the sound stimuli, the files were saved in WAV format and kept in compact discs.

2.4. Experimental procedure

Previously to the experiment, the animals had got used to eating inside the test arena and entered there spontaneously. Before each observation session we randomly chose one of the adult animals and released the others. The experimental trials started 30 minutes after the individual had been isolated.

The initial position of the subject was standardised by placing the bait (2.0kg of Napier grass) on the floor at one end of the arena (Figure 2). At the opposite end, outside the arena, we placed a speaker (model SP-D4, Japan Victor Company Ltd., Yokohama, Japan) connected by a 50m cable to a Compact Disc Player (model MS-505, Comércio de Componentes Eletrônicos, Manaus, Brazil). A camcorder (Mini DV HC30, Sony Corp., Tokyo, Japan) was used to record the behaviour displayed by the subject animal. Only one observer was positioned at least 50m away from the test arena, behind a wooden wall, apparently not disturbing the experimental subject.

Each animal was submitted to two playback trials - control playback (CP) and pups' whistle playback (WP) for one single time to avoid habituation. The subjects were first exposed to the CP, followed by the WP with an interval of at least 60 s. The playback trials (CP or WP) only started when the animal was eating. The trials occurred between 15h00 and 17h00 on non-consecutive days.

2.5. Data analysis and statistics

The Ethoplayer 1.3 software (Leo Software Inc., Toulouse, France) was used to analyse the individuals' responses during the playbacks (playback period - 27.5s each) and during a 30s period immediately after the end of the playbacks (post-playback period). Responses to control and experimental playbacks – the latency to stop eating

after the beginning of the playback and duration spent looking toward the speaker, the source of the playback – were compared through factorial ANOVAs followed by unequal N HCD test (Statistica version 7.0 - StatSoft, Tulsa, Ok, USA), when appropriate. Gender was included as an independent factor in the model.

2.6. Ethical note

This work followed the "Principles of laboratory animal care" (NIH publication No. 86-23, revised 1985) and was approved by the Committee of Ethics for Animal Use (CEUA) at the Universidade Estadual de Santa Cruz (proc. #003/07).

3. Results

The capybaras showed no change in their feeding behaviour during and just after the end of the bird vocalization, used as control playback. On the other hand, males and females equally ($F_{1, 14} = 0.94$, $P = 0.35$) stopped eating on average 2.6 ± 2.5 seconds (s) after the beginning of the pups' whistle playback. However, they did differ in the following behaviours. The females spent more time than males looking toward the speaker, the source of the pups' whistle ($17.0 \pm 12.9s$ *vs*. 3.0 ± 7.2 s; $F_{1, 18} = 7.12$, $P = 0.01$- Figure 3). Moreover, five out of the 13 females moved 4 to 6 m toward the loudspeaker, performing air olfaction, during the whistle playback. No male moved, apart from toward the Napier grass bait; they just showed a momentary interruption of ongoing behaviour (feeding) and paid attention for a few seconds to the sound source when playing the pups' whistle.

4. Discussion

Both males and females readily responded to the pups' whistle by stopping eating and looking toward the sound source, while ignoring the bird vocalisation. Females look longer than males to turn toward the sound source and tended to approach the loudspeaker when playing the pups' whistles. Thus, gender influences the intensity of the response.
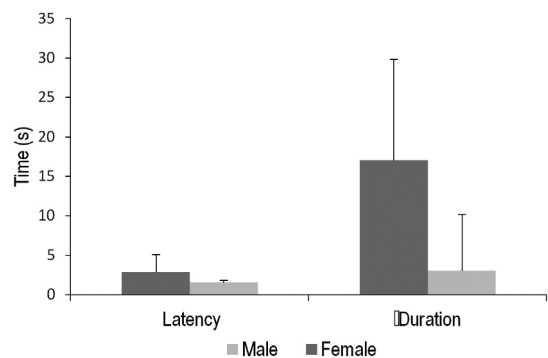
Figure 3. Mean (+SD) of the latency and duration of adult capybaras' response to pups' whistle playback, exhibited according to gender.

Unfortunately, in this experiment we could not test for responses to kin-offspring isolation calls. Despite that, all capybaras showed, at least, the interruption of ongoing behaviour (feeding) and paid attention to the sound source while ignoring the control playback. These results suggest that capybara pups' calls attract the attention of conspecifics regardless of kinship relations. Some aspects of the social structure and reproductive system of this species can contribute to a hypothesis to explain the generalised response to unrelated pups' calls. As already stated, capybara social groups are cohesive and long-lasting (Ojasti, 1973; Azcárate, 1980; Macdonald et al., 2007). Males do not care for the young directly (Ojasti, 1973; Azcárate, 1980), while females present alloparental behaviour through allosuckling – a female allows the offspring of another animal to suck her milk intentionally or by mistake (Miková and Sovják, 2005) – as well as protecting and caring for young (Ojasti, 1973; Macdonald, 1981; Nogueira et al., 2000). Besides this, pups are precocious and fully mobile form birth (Herrera and Macdonald, 1993; Herrera et al., 2011). In such a context, the sensitivity of conspecifics to the pups' whistles could promote a coordinated response to them.

This response should involve the interruption of the conspecifics' ongoing behaviour, both of males and females and, occasionally, a movement of the females toward the calling pup. Both reactions could promote the return of the isolated pup to the group with low costs to the conspecifics. We can hypothesise that the coordinated action of the individuals in the group minimises predation risks for the respondents, and consequently, the costs of responding. A similar proposal was made to explain lactating female guinea pigs' response to familiar and unfamiliar pups' isolation calls: the low cost of responding given their social structure and the precocity of the pups (Tokumaru et al., 2006).

The similarities between guinea pigs and capybaras could indicate an evolutionary trend relating to social organisation and parental care among these rodents. This hypothesis is supported by the results of Hennessy et al. (2006), who demonstrated that *Cavia aperea* females, which live in harems like *Cavia porcellus*, show socio-positive interaction with isolated unfamiliar pups. On the other hand, *Galea monasteriensis* females, which live in monogamous pairs, are mainly aggressive to them (Hennessy et al., 2006).

In our study, capybara females responded more strongly than males, which is consistent with the sexual differences in parental care in this species. On the other hand, all females were non-lactating by the time of the experiment, indicating that capybara females can respond to pups' calls independently of their reproductive state (lactating or not). Findings in other species suggest that reproductive status can influence the response to isolation calls (Ehret and Haack, 1984). However, further investigations into this effect among capybaras will help to clarify the role of reproductive status in the coordination of male and female responses to the calls of isolated infants.

Although we did not investigate the ability of individuals to discriminate between the isolation calls of different pups, this remains an interesting question that can be seen as partially independent of the response to these calls. Results for other species indicate that the ability to discriminate does not prevent a generalised response (McCulloch et al., 1999; Tokumaru et al., 2006). It seems that discrimination allows the response's modulation, as demonstrated by great spear-nosed bat females (Bohn et al., 2009). They attend to both their own and other in-group pups' isolation calls, but responses differ with conditions. The response to alien pups (stay close) seems to imply lower costs than the response to their own pup (retrieve).

Our study provides data on capybaras' social behaviour and communication, revealing that conspecifics react to unrelated pups' isolation calls. Other studies on kinship relations in the capybara group and the ability to discriminate between the isolation calls of individual pups can further contribute to understanding the costs and benefits to conspecifics and pups and the mechanisms that underlie these behaviours.

Acknowledgements

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