What Makes an Australian Sea Lion (Neophoca cinerea) Male’s Bark Threatening?

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In mammals, vocal signals are produced in many social contexts and convey diverse information about the emitter (social rank, individual identity, body size–condition). To understand their biological function, the authors find it is not only important to estimate the information about the signaler encoded in the signal but also to determine if and how this information is perceived by the receiver. In male pinnipeds (phocids, otariids, and odobenids) vocal signaling plays an important role in the breeding season during the defense of territories, females, or both. In this article, the authors investigated 2 key acoustic features that Australian sea lion (Neophoca cinerea) males most likely rely on to assess the threat level posed by potential rivals, by manipulating bark rhythmicity and spectral characteristics. Bark series that show accelerated rhythmicity and higher formants elicited stronger responses.

Keywords: vocal communication, agonistic interaction, perception, competition, pinnipeds

Animal vocal signals are produced in many social contexts, such as territorial defense, mate selection, and parent–offspring interactions (Krebs & Davies, 1993; Wilson, 1975). These signals convey diverse information about the emitter, such as species, social rank, individual identity, motivation, and body size–condition (Clutton-Brock & Albon, 1979; Fischer, Kitchen, Seyfarth, & Cheney, 2004; Reby & McComb, 2003; Schusterman, 1977; Sherman, Reeve, & Pfennig, 1997, Tripovich, Rogers, & Arnould, 2005). To better understand the biological function of a vocal signal, we find it essential to estimate not only what information about the signaler is encoded in the signal but also to decrypt it to determine if, and how, this information is perceived by the receiver (Bradbury & Vehrencamp, 1998).

The breeding season is an important period for any mammal and is when individuals may produce specific signals to advertise their social rank to other members of the group, to defend a territory or otherwise compete with potential rivals, or to ensure access to the opposite sex for breeding.

Pinnipeds (phocids, otariids, and odobenids) use vocal signals in a number of recognition processes, particularly during the breeding season (Insley, Phillips, & Charrier, 2003). Until now, studies of male pinnipeds’ vocalizations have been descriptive, focused, or both, on the acoustic parameters that might provide reliable and honest information about males’ phenotype (Kunc & Wolf, 2008; Sanvito & Galimberti, 2003; Sanvito, Galimberti, & Miller, 2007; Shipley, Hines, & Buchwald, 1981; Sjare, Stirling, & Spencer, 2003; Van Parijs, Lydersen, & Kovacs, 2003). However, few studies have experimentally tested the function of males’ vocalizations (Attard, Pitcher, Charrier, Ahonen, & Harcourt, 2010; Gwilliam, Charrier, & Harcourt, 2008; Hayes et al., 2004; Roux & Jouventin, 1987; Thomas, Zinnel, & Ferm, 1983; Tripovich, Charrier, Rogers, Canfield, & Arnould, 2008a; Watkins & Schevill, 1968), and none has examined the acoustic features effectively used by males to assess the “quality” or “threat level” of other rivals (albeit this was partially studied in Tripovich, Charrier, Rogers, Canfield, & Arnould, 2008b).

Australian sea lion males are highly aggressive during the breeding season that lasts 5–7 months (Gales, Cheal, Pobar, & Williamson, 1992; Higgins & Tedman, 1990). While mate-guarding females, males produce one main vocalization, the bark, always produced in series (Gwilliam et al., 2008) as in other
otariids (Insley et al., 2003). Competition among males for access to estrus females is very high in this species, and males produce barks to advertise their presence but also to avoid frequent fights. Barks are individually stereotyped (Gwilliam et al., 2008) and vary between colonies (Attard et al., 2010). Recently, Australian sea lion males have been shown to be able to differentiate this geographical variation (Attard et al., 2010).

In mammals, motivational state and threat are encoded in males’ vocalizations by using two main features: the calling rate and the spectral profile (i.e., peak frequencies, formants, and formant dispersion). Although other acoustic features such as call intensity and call duration might also be good and honest indicators of males’ body size, they have not been much studied. In cvrds, territorial males increase their vocalization rate during agonistic interactions with competitors or before a fight against rivals (Clutton-Brock & Albon, 1979; McElligott & Hayden, 1999). Spectral profiles also provide accurate information about the caller’s body size and fighting abilities (source-filter theory, see Taylor & Reby, 2010, for review), allowing receivers to perceive the potential threat of a rival. Vocalizations that show small formant dispersion (i.e., calls with lower frequencies) are produced by larger males (i.e., higher threat) in many mammalian species (Fitch, 1997; Reby & McComb, 2003). Preliminary observations suggested that Australian sea lion males produce barks at a faster rate when they are interacting with other rival males than when alone. Moreover, barks from bigger males appear to be composed of lower frequencies than those from smaller males (Ahonen, unpublished data). On the basis of findings on other mammals and our preliminary observations of Australian sea lions, we investigated whether bark rhythmicity, spectral characteristics, or both, can be used by males to assess the threat level posed by potential rivals.

**Method**

**Study Site and Animals**

This study was conducted in the Australian sea lion (*Neophoca cinerea*) colony on Beagle Island (29°48′48″S, 114°52′37″E), Western Australia in February–March 2010 during the breeding season. The colony on Beagle Island consists of 310 animals based on pup production of 47–79 pups between 1985 and 2004 (McKenzie, Goldsworthy, Shaughnessy, & McIntosh, 2005). Compared to other otariids species (fur seals and sea lions), the breeding colonies of Australian sea lion (and especially in Western Australia) are very low density. In 2010, the breeding male population was estimated to be between 30 and 40 mate-guarding males (Ahonen et al., unpublished data), with mate guarding males being separated from each other by 5 to 20 m. Under such low densities, the interactions between mate-guarding males are less important than in species that breed in high dense colonies. Beagle Island is a nature reserve with restricted access to avoid animal disturbance as designated by Jurien Bay Marine Park, Department of Environment and Conservation, Western Australia.

**Recording Procedure and Equipment**

Male vocalizations were recorded at close distance (5–8 m) in the colony by using a Sennheiser ME 67 shotgun microphone (Sennheiser, Wedemark, Germany; Frequency Response: 50 Hz–20 kHz ± 2.5 dB) connected to a Marantz PMD 660 digital recorder (Eindhoven, the Netherlands; Frequency Response: 20 Hz–20 kHz ± 0.5 dB; Sampling rate 44.1 kHz). Recordings of bark bouts were only performed when males were mate guarding females. Adult mature males are distinguished by their physical characteristics with a pale mane and dark brown pelage (Marlow, 1975). Mate-guarding males usually react aggressively only to males that approach closely the females they are guarding (unpublished data). A total of 12 mate-guarding males were recorded, and we obtained a number of barking bouts from each. For each male, we built three different bark series that were selected from three different bark bouts, each composed of 10 barks that showed a good signal-to-noise ratio and no overlap with other animal’s vocalizations. These different bark bouts could come from the same session or from different sessions.

**Playback Procedure**

We tested whether spectral characteristics (i.e., formant frequencies) and bark rhythmicity can affect the responsiveness of mate-guarding males and, thus, be good indicators of the potential threat level of a rival male. For each acoustic parameter (formant frequencies or rhythmicity), we built two experimental signals, resulting in the testing of four stimuli.

To assess whether bark rhythmicity can affect the responsiveness of mate-guarding males, we shortened or lengthened by 50% the duration of the interbark silence by using Avisoft-SASLab Pro (Avisoft Bioacoustics, R. Specht–Version 4.52). This resulted in a slower or faster rate of barks respectively in these two experimental series (faster and slower, Figure 1). We used these values for two reasons. First, in a study of Australian fur seal (*Arctocephalus pusillus doriferus*) males, a change of ±25% in interbark duration was too small to elicit a change in reaction (Tripovich et al., 2008b). Moreover, the modified interbark durations in this study are within the natural range of the interbark silences of Australian sea lion males (min-max values: 81 to 342 ms, with average duration = 192 ms, based on two studied populations; Attard et al., 2010).

In a similar way, we tested the impact of bark’s formant frequencies (resonance frequencies of the vocal tract) in the responsiveness of mate-guarding males. We resynthesized barks by using a PSOLA-based algorithm in Praat (Boerma & Weenink, 2005). This algorithm modifies the apparent vocal tract length and, thus, the formant frequencies by a factor k but leaves all the other acoustic parameters of the original signals such as duration, fundamental frequency value, harmonics, and intensity (for details, see Reby et al., 2005). Two experimental stimuli were synthesized: one in which the barks’ resonance frequencies were lowered by 30% and another in which they were increased by 30% (lower and higher, see Figure 1). The modifications of resonance frequencies (±30%) are mainly included in the natural range of the studied population (formant spacing ΔF values range from 981 Hz to 1442 Hz based on measurements made on 10 mate-guarding males with an average ΔF = 1121 Hz).

Each experimental stimulus consisted of three series of 10 barks separated by 3-s intervals. During each playback session, males
were tested with three different stimuli: two experimental stimuli (one of the pitch modifications and one of the barks’ rhythmicity modifications) and one control stimulus (nonmodified barks series). To avoid pseudoreplication (McGregor, 1992), each stimulus was only used once and the order of presentation of stimuli was randomized. Stimuli were broadcast by using an Edirol R-09 digital recorder connected to an amplified portable speaker, Anchor Explorer Pro (Anchor Audio, Torrance, California; Frequency Response: 80 Hz–16 kHz). The loudspeaker was placed 7–8 m from the tested male and on the opposite side of the guarded female, and the broadcast level adjusted by ear to approximately natural amplitude to simulate natural barks. Playbacks were initiated when the target male was in a relaxed state (i.e., lying down and silent). Males were given a minimum of a 3-min gap between each stimulus. A playback session was excluded from analysis if the subject was disturbed by another animal during the playback or if it interacted with another male of the colony.

**Behavioral Analysis**

For each stimulus (control–experimental), we measured males’ behavioral responses for 90 s from the beginning of the playback: latency to look (LL), latency to change posture (LPC), latency to bark (LB), latency to approach the speaker (LA), and distance of approach (DA). For approach distances, we estimate the traveled distance as a ratio between the initial position of the tested male and the speaker, so distances range from 0 to 1 (for instance, 0: did not approach, 1/2: halfway, 1: walked to the speaker). No response was assigned a default value of 90 s for latencies and 0 for distances. Responses are considered as strong or aggressive when latencies to the different measured behaviors are short and when there is a close approach toward the speaker (Attard et al., 2010). We performed one principal components analysis (PCA, varimax rotation) on all our five behavioral measures (McGregor, 1992). The PCA scores of the principal components (PC) that

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**Figure 1.** Playback stimuli tested on mate guarding males. Top: signals in which the interbark duration has been lengthened by 50% (slower) or shortened by 50% (faster) compared to the natural bark series (control). Bottom: signals in which the pitch has been raised by 30% (higher) or lowered by 30% (lower) compared to the original signal (control). Spectrograms have been performed using Seewave (Sueur, Aubin, & Simonis, 2008).
showed eigenvalues greater than 1 were then compared by using a Wilcoxon’s matched-pairs test (two-tailed test) to determine whether responses differed between experimental and control stimuli.

Results

A total of 21 playback sessions were included in our analysis during which 17 Australian sea lion males were tested. Each experimental series was tested on 10 or 11 males (i.e., each male was not tested with all four experimental series). Latencies measured for the four behavioral responses varied between the control and the four experimental stimuli (see Figure 2). During each playback session, males were always tested with a control signal and two experimental signals. If the target male was tested a second time with other experimental signals, we used a different control signal. Comparisons of behavioral responses obtained with control and experimental signals were thus performed with the appropriate control signal (of the same session). This explains why responses to control signals are different when we compared them to those obtained with experimental signals (see Figure 3), with males showing weak to very strong responses to control signals.

Shorter latencies were obtained with the control and faster signals. The most striking differences between control and experimental stimuli were observed for the distances of approach, because tested males mainly approached the speaker only during the broadcast of control, faster, and higher signals (see Figure 2).

The PCA generated 5 PCs (see Table 1), but only the first PC (PC1) showed an eigenvalue greater than 1, and thus it was kept for scores comparisons. PC1 explained 54.5% of the total variance; three out five behavioral measures were strongly correlated to PC1 (all > 0.5; see Table 1). All latencies were negatively correlated to PC1 and distance of approach positively correlated. Negative values of PC1 scores corresponded to long latencies with weak or no approach toward the speaker, and thus to weaker behavioral responses, whereas positive scores indicated short latencies and approach and thus strong responses.

Bark Rhythmicity

By comparing PC1 scores obtained with signals showing faster or slower rhythmicity to those obtained with control signals (see Figure 3), we found that males’ responses to signals with a slower...
rate were significantly different (Wilcoxon’s test: $Z = 2.134, p = .0328, n = 11$ males) whereas those obtained with a faster rate of barks were not significantly different from those elicited with the control (Wilcoxon’s test: $Z = 0.051, p = .959, n = 10$ males). Indeed, males responded more quickly to calls with faster than slower rates of barks (see latencies Figure 2). In summary, males’ responses to faster signals and to control signals were comparable, whereas those to slower signals and control were significantly different.

Bark Spectral Characteristics

By comparing PC1 scores obtained with signals that show higher or lower formants (see Figure 3) to those obtained with control signals, we found that males’ responses to signals with higher formants were not significantly different from those elicited with the control (Wilcoxon’s test: $Z = 0.866, p = .386, n = 10$ males), whereas those obtained with barks showing lower formants were significantly different (Wilcoxon’s test: $Z = 2.045, p = .041, n = 11$ males). Males responded more quickly to calls with higher than with lower formants (see latencies Figure 2). In summary, males’ responses to barks with higher formant and to controls were comparable whereas those to barks with lower formants and controls were significantly different.

Discussion

This is the first study to experimentally manipulate the information contained in the vocalizations of reproductively active male Australian sea lions while they are mate guarding. By testing males with signals in which spectral profile or bark rhythmicity was modified, we directly investigated what information is used by
males in their perception of potential threats in the vocalizations of other competing males and how they adjust their behavior in response to this threat.

In this article, we have demonstrated that barks’ rhythmicity is used by males to estimate the potential threat from a male rival. Bark series showing slower rhythmicity did not elicit strong responses (long latencies and no approach toward the speaker; see Figure 2) but when accelerated, males responded in a similar fashion to control signals. Slower rates of barks did not appear to be perceived as a potential threat signal by mate-guarding males, but triggered responses comparable to “baseline” vocal behavior (males have been seen to bark slowly even while sleeping; Charrier, personal observation). By contrast, barks emitted at a fast rate are perceived as a threat, and thus induce defensive behavior. Observations of mate-guarding Australian sea lion males show that they bark faster when other males approach to challenge them, before and after fights. Bark’s rhythmicity increases as the level of aggressiveness increase among males escalates. However, the responses obtained with faster signals were not significantly stronger than control signals, suggesting that there is a threshold at which the rate of barking signals constitutes a real threat and once a threat is perceived as sufficient, the response is initiated.

These results are consistent with previous studies on mammalian males’ territorial or resource defense. South American sea lion (Otaria flavescens) males increase their bark rate with the number of females defended and agonistic interactions among males (Fernandez-Juricic, Campagna, Enriquez, & Ortiz, 2001). Galapagos sea lions bark at higher rates when defending territories, especially at the onset of their territory tenure (Kunc & Wolf, 2008). Fallow deer bucks (Dama dama) produce higher rates of groans when other males are nearby (McElligott & Hayden, 1999), with the groaning rate reflecting the level of motivation and threat to rival males. Red deer males (Cervus elaphus) produce roars at a higher rate before a fight, reflecting their level of aggressiveness (Clutton-Brock & Albon, 1979) but also revealing fighting abilities and condition to the rival (Reby & McComb, 2003). In birds, anurans’ and insects’ calling rate tends to increase or decrease with the probability of aggressive conflict (Gerhardt & Huber, 2002; Kramer & Lemon, 1983). Accelerated calls or songs are often considered as “superstimuli” that induce more reaction (Becker, 1982). Finally, call rate can be related to the male’s dominance level. In baboons (Papio cynocephalus ursinus), males of higher rank call at a higher rates (Fischer et al., 2004; Kitchen et al., 2003) and dominant male Madagascar hissing cockroaches (Gromphadorhina portentosa) produce higher rates of hisses (Clark & Moore, 1995).

Recent studies have underlined the importance of filter-induced variations in mammalian vocalizations (Reby & McComb, 2003; Taylor & Reby, 2010). Following the source-filter theory, a voiced signal results from a source (i.e., vibrating vocal cords) being filtered in the cavities of the vocal tract. This filtering process shapes the spectral profile of the signal and produces formants (Fant, 1960). These spectral profiles are “honest,” accurate indicators of body size and age of signalers (Charlton, Zhang, & Snyder, 2009; Fitch & Reby, 2001; Reby & McComb, 2003; Sanvito, Galimberti, & Miller, 2007; Taylor, Reby, & McComb, 2010) and thus can be used by receivers to estimate the level of rivalry in intrasex competition (Charlton, Zhine, & Snyder, 2010; Reby et al., 2005; Taylor, Reby, & McComb, 2010) or the attractiveness of a potential mate (Charlton, Huang, & Swaisgood, 2009; Charlton, Reby, & McComb, 2007a, 2007b; Charlton, Reby, & McComb, 2008). Here, mate-guarding males react differently to bark series in which the spectral profile has been modified. Males responded as strongly to barks with higher formants as unmodified barks, whereas barks exhibiting lower formants elicited weaker responses. Because formant dispersion is related to body size, males responded more strongly to barks simulating small males (higher formant) than those simulating bigger males (lower formant). Similar results have been found in giant panda males (Ailuropoda melanoleuca; Charlton et al., 2010) and domestic dogs (Canis familiaris; Taylor, Reby, & McComb, 2010) but contrasts with findings in crickets and green frogs in which males strongly react to stimuli with lower frequencies (Bee, Perrill, & Owen, 2000; Wagner, 1989). By avoiding responding to signals produced by bigger males, Australian sea lion males may avoid conflicts and potential injuries that could decrease their breeding success, while increased responsiveness to small males is likely to prevent smaller males from encroaching on their females at lesser cost-risk.

There are other acoustic features not tested in this study that may also give information about the threat level of a male such as the intensity and the duration of the territorial vocalizations. Southern and Northern elephant seal males produce louder vocalizations when age and body size increases (Sanvito & Galimberti, 2003). However this might not be a reliable indicator because the perception of call amplitude is strongly dependant on the orientation and distance between the receiver and the emitter. Finally, call duration could potentially provide information about the emitter size. High-ranking male baboons produce calls at a faster rate but also call for longer bouts than low-ranking males (Fischer et al., 2004). Similar increase in call duration or calling bouts has been shown in anurans (Wells & Taigen, 1986). In vertebrates, the production of longer calls require a large lung volume and thus could be a good and honest indicator for body size and body condition, however this has been unexplored (Fitch & Hauser, 2002).

The assessment of the level of threat of a rival is extremely important in Australian sea lion males because the breeding season

Table 1
Factors Generated by a Principle Components Analysis With Four PC Derived From All Latency Response Variables

<table>
<thead>
<tr>
<th>Eigenvalues</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
<th>PC5</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.73</td>
<td>0.95</td>
<td>0.84</td>
<td>0.37</td>
<td>0.11</td>
<td></td>
</tr>
<tr>
<td>% variance</td>
<td>54.54</td>
<td>19.07</td>
<td>16.83</td>
<td>7.36</td>
<td>2.20</td>
</tr>
<tr>
<td>% cumulative variance</td>
<td>54.54</td>
<td>73.61</td>
<td>90.44</td>
<td>97.80</td>
<td>100</td>
</tr>
<tr>
<td>Correlation coefficients between PC and behavioral measures</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LL</td>
<td>−0.48</td>
<td>0.46</td>
<td><strong>0.73</strong></td>
<td>0.14</td>
<td>0.00</td>
</tr>
<tr>
<td>LPC</td>
<td><strong>0.85</strong></td>
<td>−0.09</td>
<td>0.10</td>
<td>−0.50</td>
<td>0.05</td>
</tr>
<tr>
<td>LB</td>
<td>−0.35</td>
<td><strong>0.79</strong></td>
<td>−0.50</td>
<td>−0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>LA</td>
<td>−0.93</td>
<td>−0.21</td>
<td>−0.13</td>
<td>0.13</td>
<td>−0.25</td>
</tr>
<tr>
<td>DA</td>
<td><strong>0.89</strong></td>
<td>0.26</td>
<td>0.15</td>
<td>−0.28</td>
<td>−0.21</td>
</tr>
</tbody>
</table>

Note. LL = latency to look; LPC = latency to posture change; LB = latency to bark; LA = latency to approach; DA = distance to approach. Boldface signifies p < 0.001.
is very long compared to other pinnipeds species. By avoiding unnecessary fights they limit severe injuries and wasted energy expenditure while fasting ashore during mate guarding. Energy expenditure in male pinnipeds during the breeding season is high due to the separation of breeding and feeding (Boyd & Duck, 1991), even though Australian sea lion males, like some other species (Weddell seals; Harcourt, Kingston, Waas, & Hindell, 2008), do have some opportunity to offset energy losses by foraging between periods of fasting (Marlow, 1975). Our study suggests that Australian sea lion mate-guarding males can use at least two acoustic cues, bark rhythmicity and bark spectral profile, to assess the threat level of the rivals during intrasexual interactions. Further exhaustive analyses of formants, barking rate, amplitude and duration are needed to better understand their relationship to body size and reproductive status (mate-guarding vs. nonmate-guarding males; adults vs. subadult males) and also to social context (during interactions with other males or females).

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