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Articles

Call directionality and its behavioural significance in male northern elephant seals, *Mirounga angustirostris*

Marla M. Holt[a,*], Brandon L. Southall[b,1], Stephen J. Insley[b,2], Ronald J. Schusterman[b]

[a] *Ocean Sciences Department, University of California, Santa Cruz*
[b] *Institute of Marine Sciences, University of California, Santa Cruz*

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Animals often produce sounds that are focused in a particular direction relative to the caller's orientation. Although many studies have suggested ways in which directional signal design might have behavioural significance among vocally interacting individuals, there are few direct tests using experimental approaches. During the breeding season and while fasting on land, male northern elephant seals produce airborne threat calls during dyadic interactions when competing for mating opportunities. In this study, we investigated the directional cues of these calls and tested hypotheses regarding directional signalling with respect to the behaviour of receivers during vocally mediated male agonistic interactions. We then determined effects of vocal directionality on receiver responses using an acoustic playback approach. We found that male calls had substantial directionality, particularly at higher frequencies (>1000 Hz). Subordinate males responded more strongly by retreating when the caller faced the receiver compared to when the caller was at a right angle or faced away. We also found a significant difference in responses to playback sequences with different call directivity patterns. Males displayed significantly more negative phonotaxis (i.e. moved away) in response to playbacks that simulated a caller oriented towards them compared to when playbacks simulated a caller oriented away from them. These results suggest that the directionality of threat calls provides important information about the auditory scene and spatial orientation of conspecifics and that this trait, along with the receiver's ability to extract this information, may have evolved as a consequence of its effect on the breeding success and fitness of the individual.

Animals produce many sounds that do not radiate equally in all directions. In these cases, the sound energy is focused in a particular direction that depends on the signaller's orientation (Schusterman 1978;Dantzker et al. 1999; Brumm 2002; Miller 2002; Lammers & Au 2003; Southall et al. 2003; Frommolt & Gebler 2004). The directional features of calls may provide information about the signaller's orientation relative to an individual, which would enable acoustically interacting conspecifics to act appropriately in terms of social behaviour and energetics. From a sender perspective, directing one's call towards an intended receiver maximizes the signal-to-noise ratio at the receiver while also reducing degradation effects from reverberation (Richards & Wiley 1980). For example, Brumm & Todt (2003) showed that nightingales, *Luscinia megarhynchos*, are more likely to direct their calls to intended receivers by orienting towards a broadcasting speaker playing a 'rival' call. In this way, directional signals are advantageous when the detection and reception of acoustic signals are constrained by background noise (Brumm & Slabbekoorn 2005; Holt & Schusterman 2007). Such features would be particularly important if certain signal parameters such as call amplitude are used to assess an individual's condition or social rank (e.g. Sanvito & Galimberti 2003). The directionality of acoustic signals might also affect the reception and utilization of sounds by kin, competitors or predators in ways that are biologically meaningful. For instance, omnidirectional sounds may enhance the reception to individuals in unknown locations, whereas directional sounds are expected to be more private and may consequently reduce eavesdropping (Witkin 1977; Dantzker et al. 1999; Dabelsteen 2005). The vocalizations of male red-winged blackbirds, *Agelaius phoeniceus*, differ in directionality depending on the vocalization type and the context, consistent with predictions related to communication function (Patricelli et al. 2007). Directionality of antipredator calls of several species of passerine birds also vary depending on contextual cues related to interactions with a model predator (Yorzinski & Patricelli 2010).

* Correspondence: M. M. Holt, Marine Mammal Ecology Program, National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service (NMFS), Northwest Fisheries Science Center, 2725 Montlake Blvd East, Seattle, WA 98112, U.S.A.
E-mail address: Marla.Holt@noaa.gov (M.M. Holt).
[1] B. L. Southall is now at Southall Environmental Associates, 911 Center Street, Suite B, Santa Cruz, CA 95060, U.S.A.
[2] S. J. Insley is now at the Department of Biology, University of Victoria, P.O. Box 3020, Station CSC, Victoria, BC V8W 3N5, Canada.

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From a receiver perspective, gauging the orientation of the caller through the received acoustic properties of the call can provide cues necessary to act appropriately and, in some cases, minimize costs of responding. Call directionality results from characteristics of the vocal anatomy of the animal and from shadowing effects of the body relative to the produced sound frequencies. As a function of their shorter wavelength, higher frequencies are generally more affected by this process and receivers may consequently assess caller orientation by the spectral content of the vocalization (Witkin 1977; Hunter et al. 1986). Even fewer examples of how directional acoustic signals influence receiver responses are available, with evidence being qualitative and anecdotal. For example, Bartholomew & Collias (1962) noted that reproductively competing male northern elephant seals, *Mirounga angustirostris*, of intermediate status ignore the calls of the most dominant male unless they are specifically directed at them. The majority of studies investigating the features of acoustic directionality and its importance in vocal communication have been conducted on birds and anurans, while the evidence in mammals is scant. Although some studies of mammals suggest ways in which such signal design could have behavioural significance among vocally interacting individuals (see Schusterman 1978; Miller 2002; Lammers & Au 2003), we are unaware of any studies that have directly tested the salience of call directionality on animal behaviour through quantitative and/or experimental approaches.

During the breeding season, December–March, male northern elephant seals form dominance hierarchies on land through dyadic interactions involving threat-escalating behaviour including calling, chasing and fighting (Bartholomew & Collias 1962; Le Boeuf & Peterson 1969; Le Boeuf 1974). Reproductive effort is particularly costly because seals fast throughout the terrestrial breeding period. Males lose 36% of their body mass on average over the course of the breeding season, and high-ranking males lose a higher percentage of their body mass compared to low ranking males (Deutsch et al. 1990). Because these large seals fast out of the water and, like all true seals, have limited mobility on land, vocal signalling is presumably less costly than chasing and fighting. When a fight does occur, it is almost always preceded by the production of threat calls in which the seal rears up onto its foreflippers from a prone position and produces a call or series of calls lasting several seconds with the head held back and with little movement of the body (Bartholomew & Collias 1962; Sandegren 1976). Male threat calls primarily function to repel subordinate males in this breeding system of female defence polygyny (Bartholomew & Collias 1962; Le Boeuf 1974; Sandegren 1976). Threat calls alone often elicit a response from competing males regardless of whether the caller is visually identified (Bartholomew & Collias 1962; Sandegren 1976), and males call most frequently in the hours following sunset when low light levels reduce visual reception (Schusterman & Balliet 1971; Shipley & Strecker 1986). Thus, in some instances, acoustic information is likely to be the predominant sensory cue mediating agonistic interactions among male seals. Such intrasexual competitive behaviour is probably facilitated by vocalizations containing age class and/or individual-specific signal characteristics (Shipley et al. 1981, 1986). Threat calls are described as directional when frequency-dependent differences in call strength are associated with different caller orientations (Southall et al. 2003). Vocal signalling in male northern elephant seals thus provides a unique opportunity to test hypotheses regarding the behavioural significance of call directionality in mammalian vocal communication systems. In the current investigation, we focused on receiver behaviour given the lack of experimental evidence with respect to the effects of directional acoustic signals on receiver responses.

We developed three objectives to investigate how directional acoustic signals influence receiver responses with a separate study corresponding to each objective. Our objectives were (1) to identify potentially salient directional features of male northern elephant seal threat calls by measuring call directivity patterns of these signals (study 1); (2) to investigate receiver behaviour in the context of directional signalling through observations of vocally mediated male agonistic interactions (study 2); and (3) to determine the effects of vocal directionality on receiver responses through a controlled acoustic playback experiment using threat calls recorded at different orientations (study 3).

GENERAL METHODS

Study Location and Animals

We made recordings and conducted behavioural observations and playbacks on a northern elephant seal rookery at Año Nuevo State Reserve located in San Mateo County approximately 35 km north of Santa Cruz, California, U.S.A. All data were collected during the breeding months of December through March over 4 years (2002–2003, 2003–2004, 2004–2005 and 2005–2006) on the mainland of the reserve. For studies 1 and 2, recordings and observational efforts were focused on one of the larger groups, which at the peak of the season consisted of approximately 250 females, most of which had dependent pups, and up to 30 adult and subadult males. In study 3, playbacks were conducted on males associated with the large female group and a few smaller isolated groups. We estimated male age class by the degree of each male's secondary sexual characteristics, including body size, chest shield appearance and proboscis size (Le Boeuf 1974). Individual males were identified within a breeding season from unique alpha numerical markings made with hair dye on their posterior lateral areas that were later shed during the summer moult.

Data were collected under a cooperative research use agreement between Año Nuevo State Reserve and the University of California, Santa Cruz. This investigation was conducted under U.S. Marine Mammal Permit No. 87-1743-00 of the U.S. National Marine Fisheries Service Office of Protected Resources. All protocols of this investigation were approved by the University of California, Santa Cruz Institutional Animal Care and Use Committee (the Chancellor's Animal Research Committee, CARC protocol codes Schu02.12 and Insl04.02).

STUDY 1: DIRECTIVITY PATTERNS OF MALE THREAT CALLS

In the first study, we sought to identify potentially salient directional features of male northern elephant seal threat calls by addressing the following research questions. (1) How directional are threat calls, and which frequency bands provide the most directional features? (2) Which caller orientations provide directional features that are likely to be discriminable from those of other orientations? We used clap threat calls of male northern elephant seals (Bartholomew & Collias 1962) for directivity pattern analysis. These calls are relatively loud signals that consist of short (0.1–0.5 s) broadband pulses repeated in sequences. The number of pulses produced per call typically varies within and between individuals, but the temporal patterns of the pulses are stereotyped and relatively distinct among individuals (Bartholomew & Collias 1962; Shipley et al. 1981).

Methods

We recorded calls of six adult and older subadult (SA4s; Le Boeuf 1974) males using a calibrated Neumann KMR 82i condenser shotgun microphone with a windscreen and windjammer (receiver sensitivity response ±3 dB from 100 Hz to 12 kHz) connected to