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Articles

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

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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.
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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).

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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

a Sony DC-8 DAT recorder (record level fixed at 3, sampling rate of 44.1 kHz). Multiple calls were recorded from the same individual calling at different orientations using the direction of the open mouth as a reference point. Prior to each recording, we held the microphone at a fixed angle relative to the calling animal so that the orientation of recorded calls fell into one of five direction categories: 0° (with the microphone on-axis to the calling animal), 45°, 90°, 135° or 180° (with no left/right distinction). Because sound propagation is frequency dependent, with higher frequencies being more attenuated than lower frequencies, we also recorded calls at two distances, approximately 5 and 10 m away from the opening of the caller's mouth at each angle, to establish two categories of proximity. We used a tape measure to calibrate our estimates of horizontal distance prior to data collection and then approximated each distance by eye, based on male standard body length (of approximately 4 m). During each recording, the microphone was held stationary approximately 1.6 m above the ground and at an upward angle from the researcher's shoulder (e.g. at approximately 30° for recordings at 5 m) to ensure that the microphone was pointed directly towards the opening of the seal's mouth. For analysis, we included only calls that were recorded while the vocalizing animal was in the typical upright position (i.e. propped up on foreflippers with head held up or back), and with little or no movement of the head and body during the call, to ensure that our estimates of call direction and recording height were consistent between calls and that recording height was sufficient to minimize ground effects.

Calls were digitized into wave files (at a fixed sound card input level, 16-bit resolution) and analysed using a PC based spectrum analyser (SpectraPlus, sampling rate 44.1 kHz). We analysed call spectra using relative differences in one-third octave band levels (in dB). Because only one microphone was available, we compared spectra in relative one-third octave levels for three calls of the same individual recorded at 0° to determine variability between calls recorded at the same angle and distance. Each spectrum was averaged across one pulse chosen in a consistent manner among calls and based on the following criteria: (1) recordings were made in low levels of ambient noise, (2) there were no overlapping calls from other seals on the rookery and (3) the component was produced in the middle of the call sequence. Relative overall (broadband) level of the call (in dB) was calculated by summing all one-third octave band levels from 100 Hz to 12 kHz logarithmically using the following equation:

$$L_{\Sigma}(\text{in dB}) = 10 \log \left(10^{L1/10} + 10^{L2/10} + \cdots + 10^{Ln/10} \right) \qquad (1)$$

To investigate the directionality of male threat calls, we calculated the directivity index (DI, based on two-dimensional radiation patterns; Dantzker et al. 1999) of the broadband call for all individuals. We also calculated the DI of each one-third octave band level based on relative differences in pressure between call direction categories that were averaged across individuals. The DI metric is the decibel equivalent of the directivity ratio, the ratio of the maximum intensity of observed beam to that of an omnidirectional or uniform source. We made no distinction between left and right call direction categories for 45°, 90° and 135°, because we assumed that the directivity of these calls would be bilaterally symmetrical (e.g. differences at 45° would mirror those at 315°). We used a one-sample *t* test to determine whether DI of the broadband call differed from zero (a DI equal to zero would indicate an omnidirectional signal). We also used a linear regression analysis to determine the relationship between DI and frequency. Frequency (centre frequency of each one-third octave level in Hz) was log transformed for linearity because the decibel equivalent DI value is a logarithmic unit.

While the directivity index provides quantitative information about the degree to which the acoustic power is concentrated, it does not describe the shape of the radiation pattern, nor does it quantify relative differences in amplitude between different call directions. To determine which caller orientations provide potentially discriminable directional features (i.e. relative level differences for call directions of 0° versus 45°, 0° versus 90°, 0° versus 135°, 0° versus 180°, 45° versus 90°, 45° versus 180°, etc.), we also compared directivity patterns based on relative one-third octave band levels using a two-way repeated measures ANOVA (two factor repetition) with frequency (centre frequency of 20 one-third octave band levels from 100 Hz to 12 kHz) and call direction (three calls recorded at 0° and one call each recorded at 45°, 90°, 135° and 180°) as factors for calls recorded at 5 m. The Tukey test was used to conduct pairwise comparisons if a significant difference was found (Zar 1999). For all analyses, we used two-tailed tests run in SigmaPlot 11.0 (SYSTAT, Chicago, IL, U.S.A.).

Results and Discussion

Recordings were obtained for all five call direction categories at 5 m for four adult males (marked P78, B28, Y79 and J12) and two older subadult, SA4 males (marked C37 and N56) and at 10 m for two of the four adult males (P78 and B28). All subsequent measurements were based on calls recorded at 5 m. With the exception of one older subadult male (C37), multiple calls recorded at 0° were compared for variability within the same orientation category. Figure 1 shows examples of call spectra (in relative dB one-third octave band levels) of two males at various caller orientations. In general, call spectra had a bimodal distribution with peaks centred at approximately 100 Hz and 1000 Hz for most males.

We found no significant difference in one-third octave band levels between the three calls of the same individual recorded at 0° across all frequency bands (see pairwise comparisons of ANOVA below). Therefore, we used averaged levels of all calls recorded at 0° from the same individual when calculating DI values. We found that the broadband, overall measurement (100 Hz–12 kHz) of the call had a directionality index significantly greater than zero ($\overline{X} \pm SD = 2.4 \pm 1.4$ dB, $N = 6$; *t* test: $t_5 = 4.0$, $P < 0.01$). Overall call levels were greatest in the forward direction (0°) except in one male in which levels at 45° were higher by 0.5 dB. The directivity index of one-third octave bands ranged from 0.75 to 7.3 dB. As expected, we found that DI significantly increased with increasing frequency (linear regression: $r^2 = 0.92$, $N = 20$, $P < 0.001$; Fig. 2).

We also found a significant difference in overall relative sound pressure levels (ANOVA: $F_{6,27} = 6.69$, $P < 0.001$) between calls recorded at 0° and 135°, 0° and 180°, and 45° and 180° (Tukey test: $P < 0.05$). We found a significant main effect of frequency (ANOVA: $F_{19,342} = 68.6$, $P < 0.001$), a significant main effect of call direction (ANOVA: $F_{6,342} = 29.9$, $P < 0.001$), and a significant interaction effect of frequency and call direction (ANOVA: $F_{120,342} = 10.5$, $P < 0.001$) on relative one-third octave band levels of the calls. Pairwise comparisons of three calls from the same individual recorded at 0° revealed no significant difference between one-third octave levels within the call direction factor (Tukey test: $P > 0.05$). Thus, although using estimates for call direction, horizontal distance and recording height can potentially lead to errors in measures of amplitude, we found no significant variation in amplitude across all frequency bands for calls recorded from the same individual in the same direction. In contrast, we found significant differences in one-third octave levels within the call direction factor between 0° and 90°, 0° and 135°, 0° and 180°, 45° and 135°, 45° and 180°, 90° and 135°, and 90° and 180° call directions (Tukey test: $P < 0.05$). Pairwise comparisons of one-third
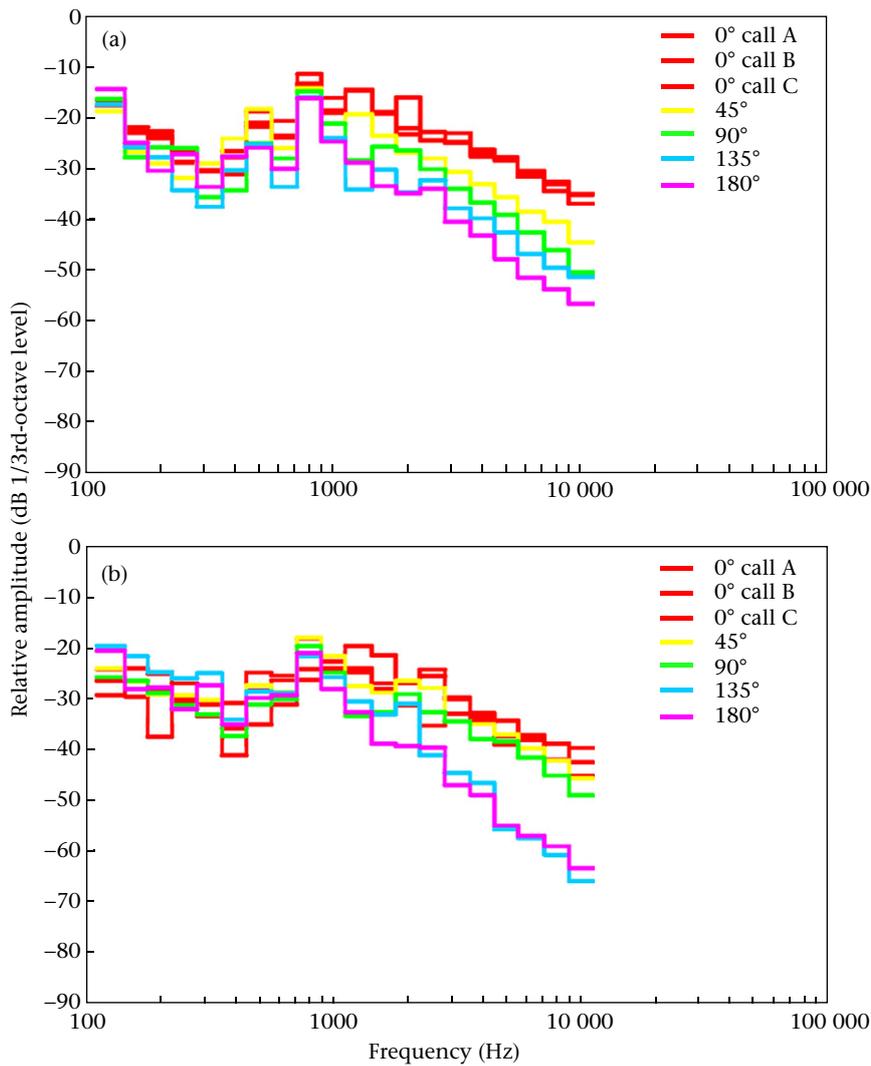
Figure 1. Directivity patterns of adult male northern elephant seals (a) 'P78' and (b) 'B28' recorded at 5 m.
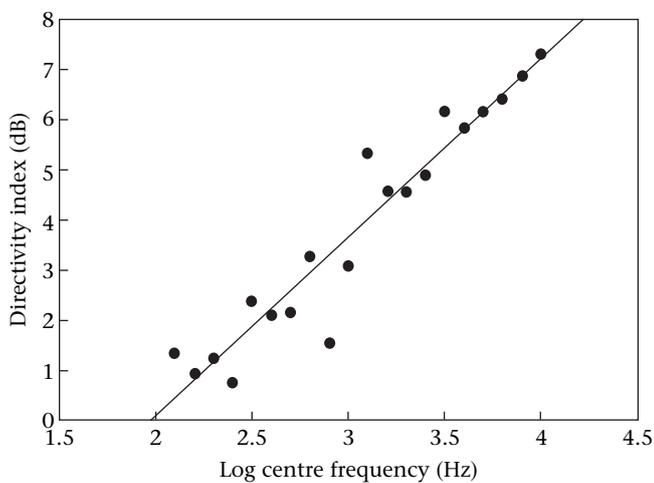

Figure 2. Linear regression of the directivity index (DI) by centre frequency of one-third octave band levels.

octave levels within the frequency factor showed no significant difference in relative level between call direction categories below 1000 Hz (Tukey test: $P > 0.05$) with the exception of the 400 and 630 Hz bands. At 1000 Hz and above, we generally found significant differences across one-third octave band levels between call direction categories (Tukey test: $P < 0.05$) except between $0°$ and $45°$, $45°$ and $90°$, and $135°$ and $180°$ (each of these were adjacent categories). Sound radiation patterns for selected mean band levels based on this analysis are shown in Fig. 3, and, as expected, illustrate that lower-frequency components of the threat call were more omnidirectional, while directionality of threat calls increased as frequency increased.

The findings of this analysis are consistent with results of other pinniped studies (Schusterman 1978; Southall et al. 2003). In general, we found that male threat calls had significant directionality given that the DI was significantly greater than zero and beamed in the forward direction. Unfortunately, our measurements were not able to address any bilateral asymmetries given that we made no distinctions between angles to the left or the right of the individual's midline. As expected, directionality increased with increasing frequency, indicating that the relative differences between call directions in higher-frequency bands probably provide significant directional features. Furthermore, we generally
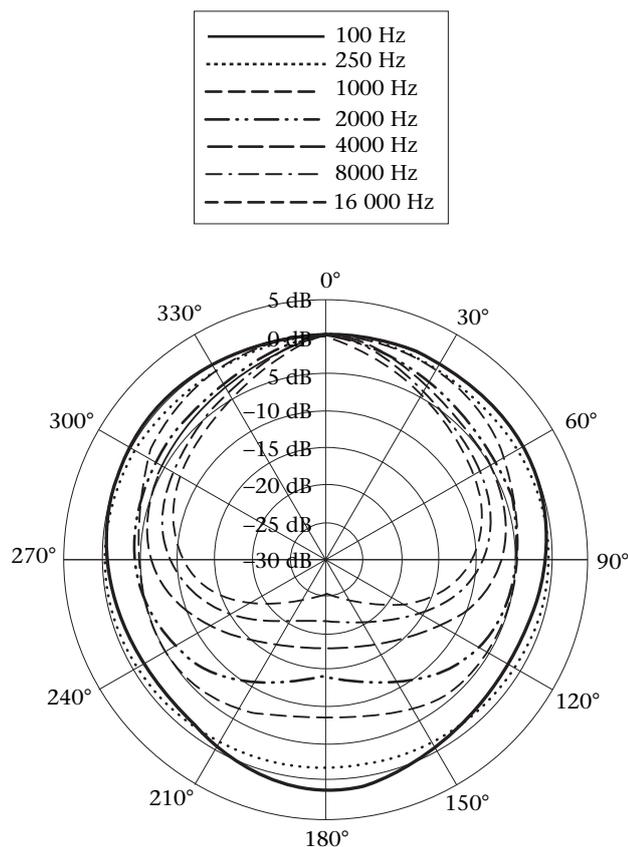
Figure 3. Radiation pattern of threat calls by adult male northern elephant seals based on selected one-third band levels (averaged from four individuals recorded at 5 m, centre frequencies shown in legend) in dB relative to calls recorded on-axis (0°). Calls were recorded every 45° and lines were smoothed (spline).

found significant differences in one-third octave levels at 1000 Hz and above for call directions separated by 90° or more. Because northern elephant seals have relatively good directional hearing in air (Holt et al. 2004, 2005) and their aerial hearing sensitivity extends beyond 20 kHz (Kastak & Schusterman 1999), it is likely that these relative differences are perceptible to free-ranging elephant seals. These differences might enable listening males to infer the orientation of the caller through acoustic information alone. Distance effects and background noise are likely to be important additional factors. While statistical differences related to call directionality were found, we conducted two additional studies (studies 2 and 3) to determine whether these differences result in significant perceptual and behavioural effects in free-ranging seals.

STUDY 2: BEHAVIOURAL OBSERVATIONS OF MALE–MALE INTERACTIONS

Given the directionality of male threat calls demonstrated in study 1, our aim in study 2 was to determine whether differences in receiver responses to threat calls depend on the caller's orientation. We hypothesized that receivers would respond more strongly to calls projected at them compared to when calls were projected at a right angle to (90°) or away from (180°) them. Bartholomew & Collias (1962) reported that dominant males ignore the threat calls of subordinates, whereas the most subordinate males retreat in response to a threat call from a dominant male, regardless of the call direction. Thus, we predicted that relative hierarchical status and distance between interacting males would influence receiver

responses. We hypothesized that subordinate males would respond more strongly to the calls of dominant males by retreating than vice versa and that responses would depend on the distance between callers and receivers, with shorter distances resulting in stronger responses.

Methods

Two field observers conducted behavioural observations 3–4 days per week over two breeding seasons, starting in the 2002–2003 season. Male–male interactions were recorded ad libitum on videotape during 0800–1100 hours or 1500–1800 hours. When a male threat call was produced, we visually estimated the caller's orientation into three easily defined categories (0°, 90° or 180° with no left/right distinction) relative to as many as three marked listening males. This corresponded to the maximum number of receivers that we could observe and score simultaneously. For simplicity, the orientation of the listener relative to the caller was not considered in the analysis. During the second breeding season (2003–2004), we also estimated the distance between callers and receivers at the time of call production to determine how this variable might influence receiver responses. Our objective was to investigate receiver behaviour in the context of directional signalling, so we focused on caller orientation as the explanatory variable, but we also collected distance estimates to control for this potential covariate during dyadic interactions.

Scoring of receiver responses and determining relative hierarchical status

Receiver responses to calls were scored into the following categories: (1) no response, (2) visual orientation in the direction of the caller, (3) rearing up from a prone position, in which the animal lifts its upper body with the foreflippers, (4) a return call, (5) positive taxis (movement towards the caller), estimated in body lengths to the nearest positive integer, (6) negative taxis (movement away from the caller), estimated in body lengths to the nearest negative integer, and (7) other. Movement was visually estimated in body lengths by using the head as a starting reference, counting the number of foreflipper pushes, and dividing this number by three. This estimate was validated by measuring the tracks made in the sand by elephant seals and comparing it to their standard body length. We scored categories of receiver responses from the beginning to the end of each call, or in the case of movement, until the receiver stopped moving (towards or away from the caller).

Our observations were focused on dyadic interactions, and for all instances, we categorized hierarchical status of a caller into a simplified, dichotomous rating system in which the caller was either dominant or subordinate to receiver. The hierarchy score was based on direct male–male interactions, including responses to movement towards females/attempted copulation, vocal threats, rearing, chases, retreats and physical contact outcomes observed throughout one breeding season (Le Boeuf & Peterson 1969). For example, if Male A visually oriented, called or moved towards Male B, and Male B showed subordination behaviours such as lying down from an upright position, turning away from or moving away from Male A, then Male A was scored as the dominant male of the dyad. If physical contact occurred, the male that retreated first was scored as the subordinate male. We included data in the analysis only when the relative hierarchical status of the two males within a dyad was unambiguous, not equal and stable over the period of our observations.

Estimation of distance between caller and receiver

Distance estimates between callers and receivers at the time of call production were determined by triangulation. We determined

the distance between a field observer and a calling seal and the distance between the field observer and a listening seal using a laser range finder (Bushnell CLR800, ±1 m accuracy). The angle between the caller and listener was determined by the field observer using a compass with a guide and bezel (Guide by Silva 426, ±0.5° accuracy). The distance between the calling male and the listening male was then estimated using these variables and trigonometric properties.

Data analysis

Although responses were scored into seven possible categories, we only considered movement by the receiver relative to the position of the caller in our analysis of receiver responses. If a response was given that did not involve movement by the receiver, such as a visual orientation, the response was scored as 0. Although this scoring method may have underestimated receiver response effects, it ensured that responses were unambiguous and that the data were within the level of a ratio scale (see below). We performed a two-way repeated measures ANOVA with caller orientation (repeated measures factor) and hierarchical status as factors, and we used a Tukey test for pairwise comparisons when a significant difference was found. Some pairs of males interacted much more often than other pairs of males given their relative hierarchical status, which resulted in a large range in the number of interactions observed among dyads (range 2–50 observations, depending on the dyad). Given the small number of adult males on the breeding site, we were limited to the number of pairwise combinations in which each dyadic interaction could be considered independent. To maximize our sample size while balancing the weight of the averaged data from the observed interactions of a dyad, all receiver data were pooled from the 2002–2003 and 2003–2004 seasons and then chosen for analysis as follows: (1) data from 16 caller–receiver dyads (eight from each season) were randomly picked using assigned numbers and a random numbers generator so that two independent receiver data points for a dyad at each caller orientation category were chosen and then averaged; (2) averages for each dyad were considered independent; (3) any one receiver could only be used twice among all dyads; (4) data were balanced for hierarchical status factor (i.e. four dominant callers and four subordinate callers relative to receivers for each of the two seasons).

Because hair-dye markings were later shed during the summer moult, we could only identify individuals within each breeding season. While the use of pet microchips and scanners have become increasingly useful methods for identifying individual pinnipeds between breeding seasons, we lacked the proper permits to microchip individuals for this investigation. Thus, we could not determine whether the same male was sampled during both seasons. We subsequently conducted an analysis using data only from the 2003–2004 field season, for which we also had data on the initial distances between callers and receivers at the onset of call production. This variable was deemed a likely covariate of receiver responses based on our observations from the first breeding season. The inclusion of this covariate, therefore, would probably increase statistical power because it would account for some of the observed variability in responses, which was desirable given the limited data available for a single breeding season. For all analyses, we used two-tailed tests run in SigmaPlot 11.0 (SYSTAT) except for the analysis of covariance, which was run in SYSTAT 9.

Results and Discussion

For data balanced at the level of the dyad and pooled across the 2002–2003 and 2003–2004 field seasons, there was a significant main effect for hierarchy (ANOVA: $F_{1,28} = 25.9$, $P < 0.001$), a marginally nonsignificant main effect for caller orientation (ANOVA: $F_{2,28} = 2.83$, $P = 0.076$), and a significant interaction effect of hierarchy and caller orientation on the distance moved by a receiver in response to a call (ANOVA: $F_{2,28} = 3.62$, $P = 0.04$). As predicted, receivers moved further from a dominant caller when the caller faced them (0°) than when the caller faced away from them (180°; Tukey test: $P < 0.05$) and when the caller was oriented at right angle (90°) to them compared to when the caller faced away from them (180°; Tukey test: $P < 0.05$). Receiver responses to a subordinate caller did not differ significantly between the three caller orientation categories (Tukey test: $P > 0.05$). If we did not consider the relative hierarchical status between interacting males, then the effects of caller orientation on receiver responses would not be apparent. In fact, the effects of a dominant receiver responding to a subordinate caller would reduce the magnitude of the effects of a subordinate receiver responding to a dominant caller.

Inspection of the 2003–2004 data showed that there was a significant correlation between hierarchical status and initial distance between the dyad such that dominant callers produced calls at shorter distances relative to receivers, while subordinate callers produced calls at larger distances relative to receivers (adjusted $R^2 = 0.19$, $F = 10.7$, $P = 0.0022$). Thus, dyad distance was incorporated into the analysis as a covariate. Controlling for dyad distance, caller orientation (ANCOVA: $F_{2,36} = 4.33$, $P = 0.021$), hierarchy ($F_{1,36} = 13.0$, $P < 0.0001$) and the interaction between caller orientation and hierarchy ($F_{2,36} = 8.7$, $P = 0.0008$) were significant factors on the response of receivers (Fig. 4).

The interaction between caller orientation and hierarchy on receiver responses corroborates descriptive accounts reported by Bartholomew & Collias (1962). The results of the current study support our hypothesis that receivers respond more strongly to calls projected at them than they do to calls projected at a right angle to (90°) or away from (180°) them, but only when relative hierarchical status and distance between interacting males are taken into consideration.
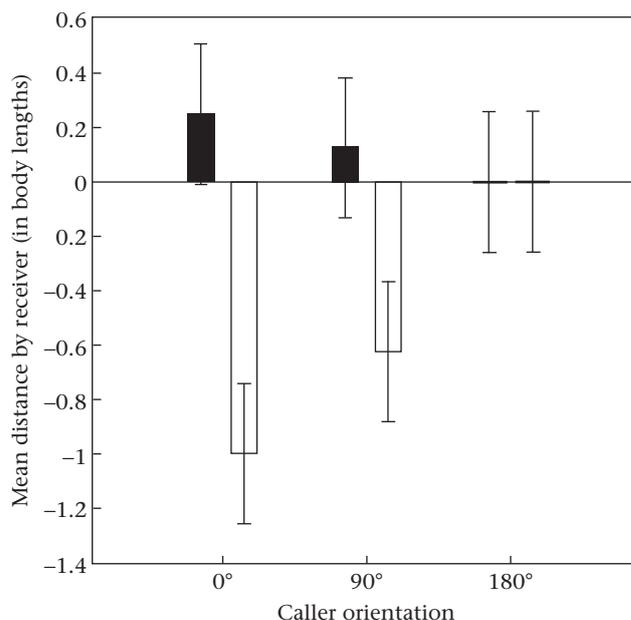

Figure 4. Mean ± SE distance moved by dominant (■) and subordinate (□) receivers for each of the caller orientation categories. Positive values on *Y* axis indicate movement towards caller, negative values indicate movement away from caller.

For seals that are fasting throughout the breeding season, moving away from a dominant caller's directed threat call and ignoring other, nondirected threat calls reduces energetic costs of responding. Furthermore, ignoring nondirected threat calls also allows a male to maintain his position among females in oestrus. At face value, the correlation between initial distance separating a dyad and hierarchical scores during vocal interactions suggests that males space themselves according to social status. More accurately, this is almost certainly related to their breeding system of female defence polygyny because the more dominant males are typically within or closer to groups of females (Le Boeuf & Peterson 1969). That is, a subordinate male moving towards a group of females also moves closer to the more dominant male. Accordingly, the more dominant males may be more likely to produce acoustic threats when the risk of a subordinate male attempting to mate with a defended female is high (i.e. at shorter distances). Alternatively, subordinate males may be more likely to produce threat calls when the risk of retaliation by a more dominant male is low (i.e. at larger distances) and/or in order to maintain vocal crypticity when close to a defended female.

STUDY 3: PLAYBACKS

Although our behavioural observations supported the hypothesis that subordinate males respond more strongly to calls projected towards them, the threat display includes acoustic as well as visual cues (e.g. stereotyped posturing during calling, as described above). Thus, we used a playback approach to isolate the acoustic component of this multimodal signal. Vocal directionality results in both overall sound pressure level and frequency component differences, so we allowed both to covary in our experimental design. We hypothesized that males would respond more strongly to call playbacks with a $0°$ directivity pattern (simulating a call projected directly towards them) than to call playbacks with a $180°$ directivity pattern (simulating a call projected away from them). We also expected that adult males would respond more strongly to playbacks (by orienting towards, calling at and/or moving towards the playback source) than would subadult males, which are typically less dominant. We conducted playbacks according to a repeated measures design within one breeding season (to reliably confirm male identity).

Methods

Playbacks were conducted between 0800 and 1800 hours, 3–6 days per week, during the 2004–2005 breeding season at one site (North Point Beach). Male elephant seal vocalizations potentially contain signal characteristics specific to age class, hierarchical status and/or individual identity (Shipley et al. 1981, 1986). To control for hierarchical status of the caller, as well as possible recognition effects, we used calls recorded from the most dominant male (marked TR7) at a different breeding site (Mid Bight Beach), well out of auditory range (ca. 1 km). This individual maintained the most dominant position among all males during the breeding season at Mid Bight Beach and was never observed at North Point Beach. Although it would have been more desirable to use calls from different dominant males to address issues related to pseudoreplication (McGregor et al. 1992), we had limited research access to other distant colonies and only male TR7 was consistently observed to be a dominant male at this breeding location. Recordings were made using the same equipment as in study 1. Multiple calls were recorded from the same individual calling at different orientations. The orientation angle for each call relative to the receiving microphone was visually classified into one of three categories: with the animal facing the microphone ($0°$), at a right

angle to the microphone ($90°$), or facing away from the microphone ($180°$). Only calls recorded between 10 and 15 m from the source and with good signal-to-noise characteristics were used for playbacks. It was impossible to avoid some overlapping vocalizations of females and pups on the rookery while recording the individual's calls because, as with most dominant males, this individual was always in close proximity to groups of females with pups. Thus, responses to playback sequences consisting of only these rookery sounds without male calls served as controls.

Playback synthesis

Calls were digitized using SpectraPlus software (16-bit resolution, sampling rate 24 kHz) and edited into playback series that consisted of one experimental sequence and one matched control sequence. Each experimental sequence contained three male call exemplars with 10 s allowed between the three call exemplars. This interval corresponds to the average timing between calls in multiple call series observed in this population. To control for variation in the number of pulses per call among exemplars, these calls were chosen such that the total number of pulses summed across the three calls was equal and all sequences were 60 s in duration. Matched control playback sequences were constructed using the same recording sequence for a given directivity condition but with all male call components removed. Control sequences were also standardized to 60 s durations by adding a few seconds of temporally adjacent background ambient noise to the beginning or end of the sequence. Three playback series were constructed. The $0°$ series consisted of three call exemplars with $0°$ directivity pattern ($0°$ experimental sequence) and its matched control ($0°$ control sequence), the $90°$ series consisted of three call exemplars with $90°$ directivity pattern ($90°$ experimental sequence) and its matched control ($90°$ control sequence), and the $180°$ series consisted of three call exemplars with $180°$ directivity pattern ($180°$ experimental sequence) and its matched control ($180°$ control sequence).

Playback procedure

Playbacks were conducted on a sample of 10 adult males and 10 older subadult males (SA4s; Le Boeuf 1974). Playback series were broadcast from recordings stored on digital audiotapes played from a Sony DAT recorder. Two two-way loudspeakers (Advent AV570, 40 Hz–20 kHz $\pm$ 3 dB) with built-in amplifiers (35 W each) were powered by a 12 V battery and placed side by side in a plastic milk crate. The loudspeakers in the crate were always placed 7 ± 1 m from and facing the focal male to control for speaker directionality effects. The relative differences in maximum sound pressure levels between the three experimental playback conditions were matched with relative differences in source level for calls from respective directions (Southall 2002; Southall et al. 2003; this study). Maximum root mean square sound pressure levels (SPL in dB re. 20 µPa) projected from the playback speaker system were measured in the field using a calibrated digital sound level meter (B&K 2230, linear weighted, fast setting). Maximum source levels were 103.2, 98.3 and 94.6 dB (re. 20 µPa @ 1 m) for the $0°$, $90°$ and $180°$ experimental playback sequences, respectively. The highest levels were dictated by the maximum output of the equipment before distortion occurred. These levels were consistent with the lower end of the source level range of adult male northern elephant seal threat calls measured at this site (Southall 2002; Southall et al. 2003; Insley & Southall 2005). Recorded rookery noise levels of the control sequence were broadcast at an overall broadband SPL that was identical to the corresponding experimental sequence. While SPLs of rookery noise might seem higher than those naturally occurring in the field, it was necessary to match the amplitude of the control sequence to the experimental sequence to address potential effects of SPL on receiver responses.

The temporal sequence of a playback series was as follows: (1) 2 min behavioural baseline observation of the focal male with the playback equipment in place; the animal had to be resting and not interacting with other animals so that observable responses to the playback were contrasted to low levels of activity and were consistent between males and conditions tested (Hopp & Morton 1997); (2) 60 s matched control playback sequence; (3) 5 min break; (4) 60 s experimental playback sequence; (5) 2 min observation. For each playback, the control sequence was always broadcast before the experimental sequence because of the predicted behavioural/contextual change during the test treatment (Grafe et al. 2002). Furthermore, attempts to counterbalance treatment order often resulted in the need to reconfigure the equipment and/or abort the test, and consequently, we deemed it problematic.

A repeated measures design was used in which each male was tested with all three playback series. To minimize habituation effects, a male was exposed to only one playback series per day. Playbacks for the 0° and 180° series were conducted first with treatment order counterbalanced until the targeted sample size for each age class was completed. These playback series were prioritized because variables associated with weather and repeated sightings of individual males were unpredictable. Therefore, the third exposure was always the 90° series for each individual.

Criteria of responses

Male northern elephant seals responded to threat calls in study 2 by visually orientating towards the source, rearing up, calling, body slamming, moving towards or away from the caller and/or physically contacting the caller.

In the present study, we scored the number of calls produced and phonotaxis (movement towards or away from the loudspeakers, estimated in body lengths, as in study 2) of the focal male during and within 2 min after the playback sequence broadcast. These two response categories were chosen as the best metrics for analysis because they were unambiguous and, apart from physical contact, were the most behaviourally significant aggressive displays during competitive interactions. All reactions to playbacks were videorecorded for further analysis.

Data analysis

Calling and phonotaxis responses were not normally distributed, so we compared playback responses among the three experimental treatment orders and among the three control and the three experimental sequences separately using Friedman tests (corrected for ties), followed by Tukey tests when significant differences were found (Siegel & Castellan 1988), for all subjects combined. We also compared phonotaxis responses of adult and subadult males separately using the same statistics. In addition, we compared responses at the beginning (first half) and end (second half) of the test period using the Mann–Whitney U test. For all analyses, we used two-tailed tests run in SigmaPlot 11.

Results and Discussion

Some adult males (6/10) responded to the playback series by calling, whereas none of the 10 subadult males responded vocally (Fisher's exact test: $P = 0.01$). There was no significant difference in the number of calls produced by adult males in response to the three experimental sequences (Friedman test: $F_{r,2} = 0.64$, $N = 10$, $P = 0.73$) or in response to the three control sequences (Friedman test: $F_{r,2} = 2.0$, $N = 10$, $P = 0.37$). Only one male responded vocally to a control sequence.

Phonotaxis did not depend on treatment order (Friedman test: $F_{r,2} = 1.7$, $N = 20$, $P = 0.43$), nor did it depend on whether the

playback was conducted at the beginning or the end of the test period (Mann–Whitney U test: $U = 421.5$, $N_1 = N_2 = 30$, $P = 0.66$). These results support the conclusion that habituation did not significantly affect responses to playbacks. Phonotaxis did not differ significantly between the three control sequences, (Friedman test: $F_{r,2} = 4.5$, $N = 20$, $P = 0.10$) but did differ significantly between the three experimental sequences (Friedman test: $F_{r,2} = 8.5$, $N = 20$, $P = 0.014$; Fig. 5), particularly between the 0° and 180° playback sequences (Tukey test: $P < 0.05$). Phonotaxis also did not differ significantly between adult and subadult males in the three experimental playbacks, but the sample size was small ($N = 10$ for both groups). Although our small sample size precluded comparison of adult and subadult responses to each playback sequence separately, both groups of males showed a tendency to display positive phonotaxis to the matched control sequences at 0° relative to 90° and 180°, probably because source levels for the control sequences were matched to those of the experimental sequences (Fig. 6). That is, rookery noise was broadcast during a playback at the relatively highest sound pressure levels for the 0° control sequence compared to the 90° and even less so for the 180° control sequences. In contrast to responses during the control conditions, subadult males tended to display negative phonotaxis to the 0° and 90° experimental sequences relative to 180°, while adult males tended to display positive phonotaxis to the 180° experimental sequences relative to 90° and 0° sequences. The largest difference observed was between adult responses to 180° playbacks and
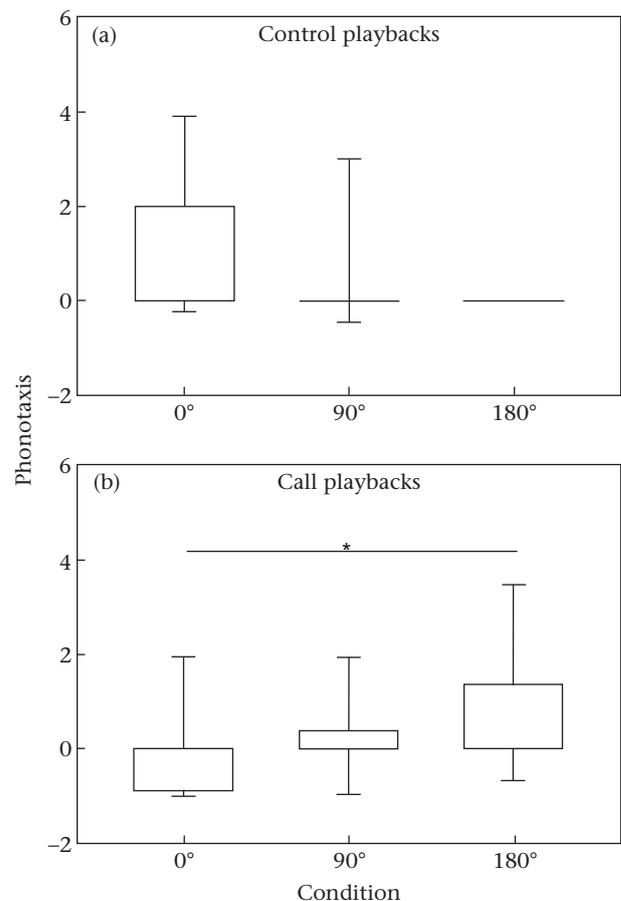

Figure 5. Box plots showing median (dark line), 25–75th percentile (box) and 5–95th percentile (whiskers) of phonotaxis estimated in body lengths for all males in the (a) three control playback sequences and (b) the three experimental (call) playback sequences. $N = 20$ for all cases, *$P < 0.05$.
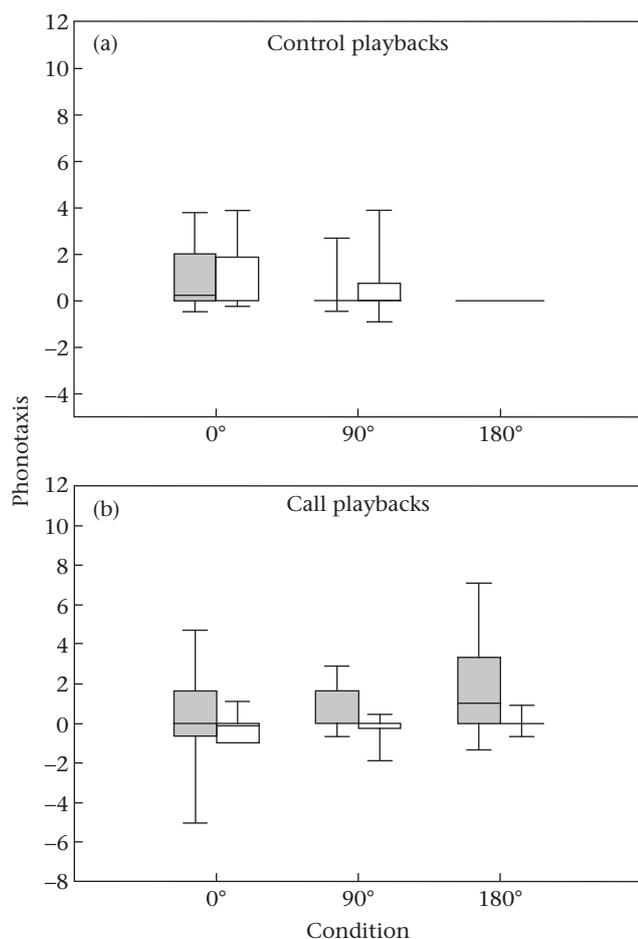
Figure 6. Box plots showing median (dark line), 25–75th percentile (box) and 5–95th percentile (whiskers) of phonotaxis estimated in body lengths for adult (▩) and older subadult (☐) northern elephant seals during (a) control playback sequences and (b) experimental (call) playback sequences. *N* = 10 for all cases.

of the male threat call significantly influence the behaviour of receivers, and they suggest that different age classes respond differently to male threat calls, but further investigation is warranted.

GENERAL DISCUSSION

During the breeding season, male northern elephant seals defend groups of females in oestrus. This system of female defence polygyny is mediated by threat-escalating behaviour that serves to delineate and maintain hierarchical status between sexually competing males. In study 1, directivity patterns and the directivity index of threat calls by four adult males and two older subadult males were determined based on five orientation categories. We found that the broadband, overall measurement of the call was greatest in the forward direction and the radiation patterns consisted of considerably less high-frequency information as caller orientation increased in azimuth away from 0°. DIs of each one-third octave band significantly increased with increasing frequency, indicating that differences in high-frequency information provide potential acoustic directionality cues. Furthermore, one-third octave levels at and above 1000 Hz were generally significantly different from each other between call directions separated by more than 45°. Because northern elephant seal hearing sensitivity in air extends beyond 20 kHz (Kastak & Schusterman 1999) and because their hearing is quite directional (Holt et al. 2004, 2005), it is likely that these differences are perceptible to free-ranging elephant seals.

We conducted studies 2 and 3 to determine whether these differences in radiation pattern related to caller orientation resulted in significant perceptual and behavioural effects from the perspective of a receiver. The results of our behavioural observations in study 2 illustrated that caller orientation significantly influenced responses of listeners, but other variables are also important. One variable is relative hierarchical status between interacting males. In particular, subordinate male receivers retreated further from a dominant caller that was oriented towards them as opposed to away from them. In contrast, receiver responses did not depend on caller orientation when the caller was subordinate to the receiver. The correlation between initial distance separating a dyad and hierarchical scores during vocal interactions was an interesting result that, to the best of our knowledge, has yet to be described in the literature. We found that dominant males produced threat calls at shorter distances from receivers than did subordinates, presumably when the risk of a subordinate male attempting to mate with a defended female was high. In contrast, subordinate males produced threat calls at longer distances from receivers, when the risk of retaliation by a dominant male was low. It is also likely that subordinate males may not produce threat calls when close to a dominant male in order to maintain vocal crypticity, which would increase mating opportunities.

Because male northern elephant seals usually rear up while producing a call, responses to calls might also reflect directional information visually perceived by the receiver. However, males responded to acoustic playbacks (study 3) similarly in the absence of such visual information. In particular, the responses of subordinate listeners in study 2 and those of subadult subjects in playback experiments (study 3) were very similar when call directionality was considered, particularly between 0° and 180° caller conditions. The acoustic cues of the playbacks included overall sound level effects as well as relative differences in higher-frequency components, as illustrated in study 1. It is unknown whether males were responding to differences in one or both of these acoustic parameters of the playbacks. Study 1 demonstrated that the overall amplitude of the threat call differed significantly only between

subadult responses to 0° playbacks (Fig. 6). Potential differences in responses between these age classes, however, will require further investigation with a larger sample size and greater statistical power.

Only adult males produced calls in response to playback sequences and although not statistically significant, the majority of these calls were produced during experimental playback sequences (containing male calls, 5/6) compared to control sequences (without male calls, 1/6). There was a significant effect of phonotaxis that corroborated results of observational data collected at the same study site in study 2. That is, males responded more strongly with a tendency to display negative phonotaxis to call playbacks having 0° directivity patterns relative to those with a 180° directivity pattern. There were two levels of potential pseudoreplication to address in this study. One being the number of playback call exemplars from an individual and the other being the number of individuals represented. The first issue was explicitly dealt with by using multiple call exemplars for each playback treatment. The second issue was problematic because of the need to control for social factors and because there were only a few 'unfamiliar' dominant males. The playbacks contained multiple calls from only one individual, so generalizations about how receivers might respond to the directional features of other callers cannot be addressed from this investigation. These playback responses illustrate that the isolated acoustic variables of the directional features

0° and 135° and between 0° and 180°. Male phonotaxis responses also differed significantly between 0° and 180° (135° was not tested) in studies 2 and 3, indicating that the acoustic aspects of directionality affect receiver responses. Responses of listening males are likely to be strongly affected by amplitude because more dominant males tend to produce calls with higher source levels (Sanvito & Galimberti 2003; Insley & Southall 2005). Future playback studies aimed at separating the relative contributions of amplitude and frequency are necessary to determine which of these variables, either alone or in combination, has a stronger influence on receiver response. The results of the present study, however, strongly suggest that the directionality of calls provides important acoustic information to male northern elephant seals in reproductive competition.

Previous studies on acoustic directionality of animal vocalizations have mainly focused on descriptions of sound radiation patterns and hypothetical ways that directional signals might have behavioural importance (Witkin 1977; Dantzker et al. 1999; Miller 2002; Lammers & Au 2003). Recent studies that have tested hypotheses about the behavioural significance of acoustic directionality have focused on the significance of caller behaviour, with the vast majority focused on vocal communication in birds (Brumm & Todt 2003; Patricelli et al. 2007; Yorzinski & Patricelli 2010). Acoustic communication, like any mode of communication, involves at least one sender and one receiver. There are many interpretations regarding the functions that communication serves in animal interactions, one being how the sender's signal influences the behaviour of the receiver. Related to this is how the features of the signal, such as temporal or spectral cues, influence receiver responses (e.g. Rendall et al. 2009). Another signal feature to consider in this respect is its directionality.

In the present study, we present quantitative and experimental evidence that the directionality of threat calls of male northern elephant seals influences the behaviour of receivers. From the receiver's perspective, ignoring nondirected threat calls minimizes costs of responding and allows the male to maintain or, in the case of the caller facing away, augment his position among females in oestrus. Inferring the orientation of the caller through acoustic properties of the call has the potential to mediate appropriate response behaviour that potentially minimizes costs of responding and maximizes reproductive effort. The individually distinct, stereotyped threat calls of males promote individual recognition among these sexually competing males (Shipley et al. 1981) and, together with the directional properties of the calls, contain important information that influences receiver behaviour. These results seem congruent with modes of behaviour that both conserve energy for animals fasting during the breeding season and that maximize mating opportunities for males defending groups of females. In the absence of visual information, the directional design of the male call as a component of a sexual display signal may have evolved as a consequence of its effect on the breeding success and fitness of the individual. Our results suggest that behaviours that capitalize on the directionality of these acoustic signals are common among male northern elephant seals and that such acoustic cues provide important information about the auditory scene surrounding an individual.

Acknowledgments

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