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ORIGINAL PAPER

Geographic vocal variation and perceptual discrimination abilities in male Australian sea lions

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Abstract

Vocal characteristics can vary among and within populations. In species with geographic variation in the structure of vocalizations, individuals may have the ability to discriminate between calls from local and non-local individuals. The ability to distinguish differences in acoustic signals is likely to have a significant influence on the outcome of social interactions between individuals, including potentially mate selection and breeding success. Pinnipeds (seals, fur seals, sea lions and walruses) are highly vocal yet the Australian sea lion (*Neophoca cinerea*) is the only eared seal known to show geographic vocal variation in male barks. Barks are produced in many social interactions and encode sufficient information for both individual and colony identity to be discriminable. Yet until now, whether males could themselves discriminate these bark differences was unclear. We performed playback experiments in four breeding colonies to investigate whether males can discriminate local from non-local barks. Overall, males responded more strongly to barks from their own colony compared to barks from other colonies regardless of whether those other colonies were close or distant. Competition for females is high in Australian sea lions, but mating periods are asynchronous across colonies. The ability to correctly assess whether a male is from the same colony, thus representing a potential competitor for mates, or merely a visitor from elsewhere, may influence how males interact with others. Given the high cost of fighting, the ability to discern competitors may influence the nature of male–male interactions and ultimately influence how they allocate reproductive effort.

Keywords Acoustic behavior · Vocal recognition · Pinniped · Otariid · *Neophoca cinerea* · Perceptual discrimination

Introduction

When animals occupy a wide or discontinuous range, geographic variation in vocal and other signals may arise (Conner 1982). This geographic variation in vocalizations can be a result of several, not necessarily mutually exclusive factors, including differences in the physical environment and morphological traits, vocal learning, isolation and drift or as a consequence of sexual selection to mediate breeding behavior (Wilkins et al. 2013). Differences in vocalizations can also maintain and reinforce genetic divergence, and demonstrably play an important role in speciation processes (Slabbekoorn and Smith 2002; Ellers and Slabbekoorn 2003; Wilkins et al. 2013).

Geographic variation in bird songs or calls may influence sexual and social interactions, such as the ability of males to attract females or to establish and maintain a territory (Kroodsma et al. 1984; Baker and Cunningham 1985; Slabbekoorn and Smith 2000; Ellers and Slabbekoorn 2003). A classic study of white-crowned sparrows, *Zonotrichia leucophrys*, reported that females show stronger responses to local dialects (Baker et al. 1981; Baker 1982, 1983; Lampe and Baker 1994) and since then it has been reported that in most bird species, territorial males also respond more strongly to local dialects (e.g., Baker et al. 1981; Tomback et al. 1983; Searcy et al. 1997; Mortega et al. 2014). Males with less familiar song characteristics may be less efficient

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in using songs to deter competitors, and this may then result in reduced success in establishing a territory (Jenkins 1978; Baker 1982), and thus reduce breeding success. This suggests that non-local males are likely to be less successful and therefore pose less of a threat in male–male competition. Hence, the ability to distinguish between true competitors and non-competitors can have significant fitness consequences.

Geographic vocal variation appears widespread in many taxa, not just in birds (e.g., Wilczynski and Ryan 1999; Zuk et al. 2001; Catchpole and Slater 2003; Yu et al. 2011; Lee et al. 2016) but also mammals (Conner 1982; Janik and Slater 1997). Pinnipeds (seals, fur seals, sea lions and walrus) tend to breed in clustered colonies on islands, isolated beaches or on sea ice (Riedman 1990). Vocalizations have important social functions and geographic variation in male pinniped vocalizations appears widespread, mapping their clustered distribution. Geographic differences in male vocal repertoire and/or vocalization characteristics have been shown in seven species of phocid (earless or true seals) but only in one otariid (eared seals or fur seals and sea lions) the Australian sea lion, *Neophoca cinerea* (Table 1).

In Australian sea lions, males mate-guard one or a small group of females at a time (female defense polygyny; Boness 1991) and breeding is asynchronous between colonies (Gales et al. 1994; Shaughnessy et al. 2011; Ahonen et al. 2016). While mate-guarding, males remain close to females and aggressively prevent other males from approaching, actively herding females until estrus and successful mating. Australian sea lion males produce barks in most social interactions including male–female and male–male dyadic encounters. The male bark is a short noisy sound, produced repetitively in series but with sufficient embedded information to provide the potential for individual discrimination (Gwilliam et al. 2008). In a preliminary study (Attard et al. 2010) we found that male barks vary significantly between two geographically distant colonies (separated by 180 km) and more importantly, that mature males were able to perceive these vocal differences. The main source for these differences was hypothesized to be reproductive isolation induced by strong site fidelity and large geographic distance. Both male and female Australia sea lions are found to be highly philopatric with limited dispersal and gene flow between colonies (Campbell et al. 2008; Lowther et al. 2012; Ahonen et al. 2016). Male Australian sea lions are capable of long-range movements (up to 368 km, Gales et al. 1992; Lowther et al. 2013); however, a recent genetic study only detected individual male dispersal between close colonies (< 110 km, Ahonen et al. 2016).

We predicted that acoustic variation in male barks would be greater between distant colonies than within nearby colonies leading to more accurate discrimination of male barking calls from distant colony than close by colony. We selected Australian sea lion breeding colonies across the species range to investigate the extent to which males can discriminate barks from among colonies. At the time of the study design and playback experiments, we did not know that the pattern of male bark variation in the Australian sea lions was not this straightforward and we performed our acoustic variation study and playback study simultaneously (Ahonen et al. 2014). Barks vary significantly among breeding colonies, both on micro- and macro-geographic scales; however, neither genetic differences nor geographic distances could fully explain this observed acoustic variation (Ahonen et al. 2014). Here we present results from playback experiments conducted on four breeding colonies. We investigate the ability of male Australian sea lion to discriminate between local male barks and non-local barks and more importantly between barks from nearby and distant colonies.

Materials and methods

Study sites and animals

We performed playback experiments on four Australian sea lion breeding colonies (see Supplementary figure 1). Three of these colonies, Olive Island, Liguanea Island and Lewis Island, are situated along the southern coast of South Australia (SA). The fourth colony, Beagle Island,

Table 1 Pinniped species showing geographic variation in male vocal repertoire and/or vocalization characteristics

Common name	Specific name	Source
Australian sea lion	*Neophoca cinerea*	Attard et al. (2010) and Ahonen et al. (2014)
Bearded seal	*Erignathus barbatus*	Cleator et al. (1989) and Risch et al. (2007)
Harbor seal	*Phoca vitulina*	Bjørgesæter et al. (2004), Van Parijs et al. 2000, 2003)
Harp seal	*Pagophilus groenlandicus*	Perry and Terhune (1999)
Leopard seal	*Hydrurga leptonyx*	Thomas and Golladay (1995)
Northern elephant seal	*Mirounga angustirostris*	Le Boeuf and Petersen (1969) and Le Boeuf and Petrinovich (1974)
Ribbon seal	*Histriophoca fasciata*	Mizuguchi et al. (2016)
Weddell seal	*Leptonychotes weddellii*	Abgrall et al. (2003), Terhune et al. (2008) and Thomas and Stirling (1983)

is off the western coastline of Western Australia (WA). Experiments were carried out during the 2009–2010 and 2010–2011 breeding seasons. For data integrity, only adult mate-guarding males were selected for both recording and playback experiments. Adult mature males are distinguished by their physical characteristics with a pale mane and dark brown pelage (Marlow 1975). Males were identified through natural markings (e.g., scarring, flipper tears and marks) in order to avoid the possibility of replicated sampling and testing. Furthermore, most males were also genetically sampled and individual identification was confirmed through microsatellite genotyping (see Ahonen et al. 2016 for details).

Recording procedures

Male barks were recorded from five colonies, from which four (i.e., all except Kangaroo Island) were tested with playbacks (see Supplementary figure 1). These recordings were used as local stimuli as well as non-local stimuli for other tested colonies (see Table 2 for details on the different playback stimuli and experimental design). Recorded barks were also used to quantify acoustic variation among colonies, in order to evaluate the degree of acoustic distances among the studied colonies.

Male barks were recorded at close distance (3–8 m) 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: 22.05 kHz). To avoid significant differences in barking rate (duration between barks) due to motivational state of the recorded male, recordings were done in similar circumstances (when mate-guarding males had been disturbed by another animal or were interacting with the female they were guarding).

Playback stimuli selection

We selected natural bark series from 66 mate-guarding males for playback experiments: 11 from Kangaroo Island (KI), 15 from Lewis Island, 10 from Liguanea Island, 18 from Olive Island and 12 from Beagle Island. For each male, we built three different bark series that were selected from three different bark bouts, each composed of 10 high-quality barks with no overlap with other animal's vocalizations. These different bark bouts could come from a same recording session or from different recording sessions. A total of 198 bark series were used in our playback experiments.

Playback experiments

Our initial hypothesis and study design predicted that acoustic variation in male barks would be greater between distant colonies than within nearby colonies. Hence, when possible we tested local males with three series of barks: one series composed of barks from local males, one series with barks from a nearby colony (i.e., < 50 km apart) and one series with barks from a distant colony (i.e., between 300 and 500 km apart) or super distant colony (i.e., > 2000 km). At the time of the playback experiments, we were not able to obtain nearby colony barks for Olive and Beagle Islands. For Olive Island, we only had barks available from two distant colonies (Lewis Island = 349 km and Kangaroo Island = 460 km). For Beagle Island, we did not have barks available from any other Western Australian colony, and hence, we only tested males with barks from a distant colony from South Australia (Olive Island) classifying this as "super" distant colony (2400 km). Table 2 describes the study design for the playback experiments. To avoid pseudoreplication (McGregor 1992), each bark series was used once in a given test colony, and the order of presentation for local and non-local bark series were randomized except on Olive Island and Lewis Island where we had more testable males than available playback series and we had to use the same stimulus twice (Olive Island: two KI bark series were used twice; Lewis Island: one Liguanea bark series was

Table 2 Study design for playback experiments

Test colony	Colony distance and bark location				*N* tested males
	Control (local)	+ (< 50 km)	++ (300–500 km)	+++ (> 2000 km)	
Lewis Is (SA)	Lewis	Liguanea	Olive	–	11
Liguanea Is (SA)	Liguanea	Lewis	Olive	–	9
Olive Is (SA)	Olive	–	Lewis, KI	–	13
Beagle Is (WA)	Beagle	–	–	Olive	14

Males from test colony where subjected to three different playback stimulus: control, +, ++, +++. Plus sign indicates increasing distance between colonies. For Olive Island we only had two distant (++) colonies, and for Beagle Island only one "super" distant (+++) colony was used

KI Kangaroo Island (SA), *SA* South Australia, *WA* Western Australia used twice). A total of 47 males were tested (see Table 2) during this study.

Stimuli were broadcast using an Edirol R-09 digital recorder connected to an amplified portable speaker, Anchor Explorer Pro (frequency response: 80 Hz–16 kHz; Anchor Audio, Torrance, CA, USA). The loudspeaker was placed 7–8 m from the tested male, and the broadcast level adjusted by ear to approximately natural amplitude to simulate a natural vocal behavior. Playback tests were initiated when the target male was in a relaxed state (i.e., laying down and not interacting with other conspecifics). Males were given a minimum 5-min gap between each playback series (all males were tested with three series in a given playback session, except for Beagle Island males that only received two series). A playback session was excluded from analysis if the subject was disturbed by another animal during the playback.

We followed the same behavioral analysis previously used with Australian sea lion males (Attard et al. 2010; Charrier et al. 2011). For each playback series, four behavioral responses were observed for 60 s from the beginning of the playback series: (1) latency to look toward the speaker (LL); (2) latency for posture change (LPC); (3) latency to vocalize (LV) and (4) latency to approach the speaker (LA). Male responses were scored from 1 to 60 s and no response was assigned a default value of 60 s (see Supplementary Table 1 for frequencies of each of the four behaviors). Responses were considered strong when latencies to the different measured behaviors were short.

A principal components analysis (PCA) was then performed on these four behavioral measures (McGregor 1992) for all the tested males from the four study colonies. The PC scores of the principal components (PC) showing eigenvalues greater than 1 were then compared using Wilcoxon matched-pair tests to determine whether responses to the control (barks from local males) differed from those obtained with barks from non-local colonies (+, ++, +++; see Table 2). The Holm's procedure for Bonferroni correction was applied for multiple comparisons. Next, we focused on each study colony, and we compared the males' behavioral responses toward the local and non-local males' barks.

Assessment of acoustic differences

High-quality recordings are essential to obtain accurate measurements for acoustic parameters. Australian sea lion colonies are noisy environments, and recordings are often hindered by abiotic and biotic noises (Charrier et al. 2009; Pitcher et al. 2012). As a result, we were able to use barks from 49 males to measure differences in acoustic parameters among tested colonies (number of males per each colony: Kangaroo Is. 12, Lewis Is. 10, Liguanea Is. 8, Olive Is. 10 and Beagle Is. 9). For each male two different series of 10 consecutive barks were selected. Five variables were measured using Avisoft SAS Lab Pro (R. Specht, Avisoft Bioacoustics, Berlin Germany): bark duration (Dur, ms), inter-bark duration (InterDur, ms), the first two energy peaks (Peak1-2, Hz) and their ratio in amplitude level (RAMP1). All the details on these acoustic measurements are described in Ahonen et al. (2014).

A discriminant function analysis (DFA) was performed to assess differences in barks among five study colonies. The assignment of barks to the different colonies was cross-validated by the leave-one-out method. The squared Mahalanobis distances between the group centroids (i.e., sampling locality) were derived from DFA and used as measures of bark divergence/similarity among colonies (Ahonen et al. 2014). Correlations between both acoustic and geographic distances (calculated as the shortest swimming distance between colonies, in km) with the strength of responses (PC scores) were tested using the Pearson method. Average PC scores were calculated for each colony for these analyses. All statistics were performed using Statistica version 8 (Statsoft Inc, 2007) and R (R Core Team 2015).

Results

Playback experiments

A total of 127 playback tests were performed on 47 males from four different breeding colonies. The PCA based on the four behavioral measures extracted four PCs, but only the first one (PC1) showed an eigenvalues greater than one, and thus was used for PC scores comparisons (see Supplementary Table 2). PC1 explained 57.4% of the total variance, and the four behavioral measures were strongly negatively correlated to PC1 (all > |0.5|). Positive PC scores indicate short latencies, and thus a strong behavioral response to the stimulus, whereas negative PC scores indicate long latencies and thus a weak or no response.

Our results show that males' reactions were significantly weaker to barks from any non-local colonies (either nearby or distant colonies) than to barks from their own colony (i.e., control; Table 3). When focusing on each tested breeding colony, we found the following results.

Males from Beagle Island reacted significantly more strongly to barks from local males than males from Olive Island (Fig. 1a and Table 4).

Males from Olive Island reacted significantly more strongly to barks from local males than to those from the two distant colonies. Moreover, responses elicited by Kangaroo Island male barks were weaker than those triggered with Lewis Island barks (Fig. 1b and Table 4).

For males from Lewis Island, we obtained the opposite pattern. Surprisingly Lewis Island males reacted as strongly to local barks as to barks from distant colony (Olive Island,

Table 3 Comparison of behavioral responses to male barks from non-local colonies (+, ++ and +++) and to barks from the local colony (control) using Wilcoxon matched pairs tests

Control versus	*N*	*Z*	*p*-level
+ (< 50 km)	20	2.634797	0.008419
++ (300–500 km)	46	3.674098	0.000239
+++ (> 2000 km)	14	2.416895	0.015654

The Holm's procedure for Bonferroni correction was applied for multiple comparisons. Plus signs indicate increasing distance between colonies

349 km away), but their behavioral responses were significantly weaker to barks from the nearest colony (Liguanea Island, 48 km away) (Fig. 1c and Table 4).

Finally, playback tests on Liguanea Island showed that males did not show any significant differences in their behavioral responses to barks from local, near or distant colonies (Fig. 1d and Table 4).

Vocal differences among colonies

The cross-validated DFA performed on the five acoustic variables revealed that barks from the 5 different colonies can be correctly assigned to a colony with an average classification rate of 42.2%, i.e., higher than expected by chance (16.3–24.5% depending on colony, see Table 5). For Kangaroo, Lewis, Olive and Beagle Islands the percentages of correct classification were clearly above chance (66.7, 36.0, 38.5 and 57.8%, respectively, see Table 5). By contrast, for Liguanea Island the average correct classification rate was very low, only 6.25%.

To quantify the acoustic similarity between study colonies, we extracted acoustic distances between colonies using the squared Mahalanobis distance. We found greater vocal differentiation between South and Western Australian colonies than within South Australian colonies (Table 6, all distances > 1.99). Among South Australian colonies, the acoustic distances were relatively low

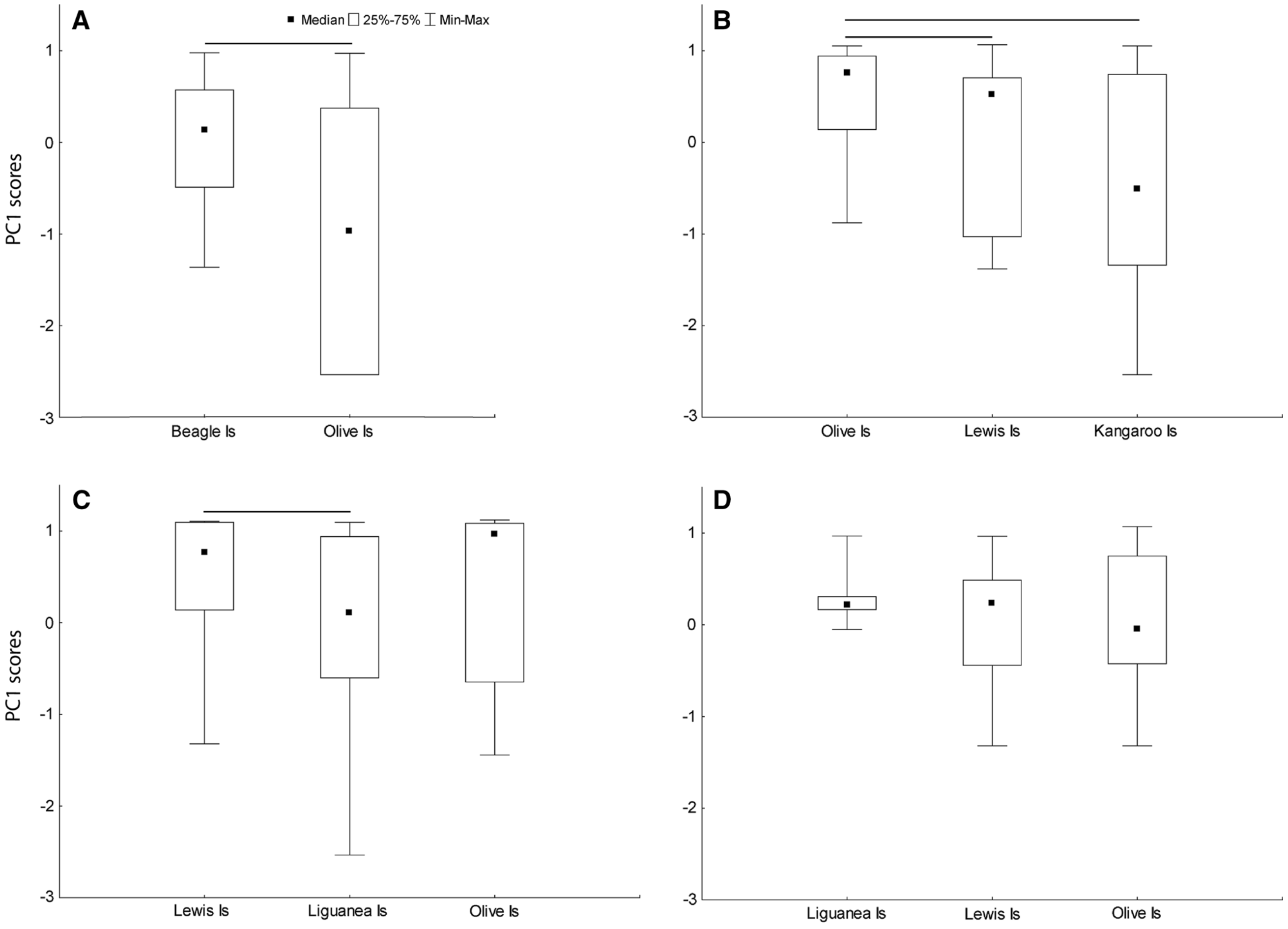

Fig. 1 PC scores for male behavioral responses to control (local colony) and non-local colony obtained for each tested colony: **a** Beagle Island, **b** Olive Island, **c** Lewis Island and **d** Liguanea Island. A horizontal bar over the PC scores of two different island locations indicate a significant difference

Table 4 Summary table of p values for Wilcoxon matched pairs test, geographic distances and acoustic distances between each test colony (control) and playback colonies (nearby/distant colony)

Test colony	Playback stimulus	N	Comparison to control (p values)	Geographic distance (km)	Acoustic distance
Beagle Is	Olive Is	14	**0.0156**	2400	3.01
Olive Is	Lewis Is	13	**0.0464**	349	0.86
Olive Is	Kangaroo Is	13	**0.0057**	460	0.90
Lewis Is	Liguanea Is	11	**0.0152**	48	0.35
Lewis Is	Olive Is	11	0.3863	349	0.86
Liguanea Is	Lewis Is	9	0.2135	48	0.35
Liguanea Is	Olive Is	9	0.1386	301	0.34

Values in bold are significant at $p < 0.05$

Table 5 Correct classification rates of male Australian sea lion barks obtained for the five sampled colonies using a cross-validated DFA

Barks assignment	Colonies				
	Kangaroo Is	Lewis Is	Liguanea Is	Olive Is	Beagle Is
Kangaroo Is	**160**	78	67	62	13
Lewis Is	48	**72**	28	31	42
Liguanea Is	1	0	**1**	3	1
Olive Is	25	28	30	**77**	20
Beagle Is	6	22	34	27	**104**
N total	240	200	160	200	180
% correct	**66.7**	**36**	6.25	**38.5**	**57.8**
% by chance	24.5	20.4	16.3	20.4	18.4

Table 6 Acoustic distance matrix for the five Australian sea lion colonies

	Kangaroo Is	Lewis Is	Liguanea Is	Olive Is
Kangaroo Is	-			
Lewis Is	**0.77**	-		
Liguanea Is	**0.33**	**0.35**	-	
Olive Is	**0.90**	**0.86**	**0.34**	-
Beagle Is	**4.73**	**1.99**	**2.81**	**3.01**

Squared Mahalanobis distances derived from the DFA. Cases highlighted in gray indicate colonies involved in playback experiments

(all < 1, Table 6), but varied between colonies ranging from 0.33 to 0.90. Acoustic distance and strength of the behavioral response (Table 7) were significantly correlated ($r = -0.8178$; $p = 0.013$) showing that behavioral responses get weaker when acoustic distances increase (i.e., when acoustic dissimilarity increases). Similarly, geographic distance and strength of response (Table 7) were found to be significantly correlated ($r = -0.82$, $p = 0.012$). However, this is mainly because both acoustic distance and geographic distance between the two study regions Western Australia and South Australia are very large. If we look only at the South Australian regional scale (excluding playback tests on Beagle Island), then these correlations are no longer significant.

Table 7 Acoustic distances, geographic distances and average PC1 scores between colonies

Colonies	Acoustic distances	Average PC1 scores	Geographic distance (km)
Olive/Lewis	0.86	− 0.031832	349
Olive/KI	0.90	− 0.496852	460
Liguanea/Lewis	0.35	− 0.000275	48
Liguanea/Olive	0.34	0.027788	301
Lewis/Liguanea	0.35	0.031733	48
Lewis/Olive	0.86	0.388033	349
Beagle/Olive	3.01	− 0.895124	2400
Local/Local	0	0.318	0

Discussion

Here we have shown that male Australian sea lions have the ability to discriminate between local and non-local barks, despite the apparent simple structure of male bark. The ability to discriminate among neighbors, who are potential rivals for mates, and conspecifics that may be passing through a colony and so pose less of a competitive threat has direct and realizable advantages, discussed below.

Behavioral response, acoustic similarity and geographic distance

While we have shown that males have the ability to discriminate dissimilar barks, the responses were neither uniform nor linear. Overall, males responded more strongly to barks of their own colony (i.e., local barks) than to barks from other colonies. However, we did not find that the strength of male discrimination was related to the geographic distance between colonies (i.e., weaker response toward barks from distant than from nearby colony). Nor were we able to conclude that acoustic similarity/dissimilarity uniformly explained the different male responses to non-local colonies.

On Beagle and Olive Islands, we could only use distant colonies as a playback stimulus and results from these two colonies clearly showed significantly stronger responses to local male barks than to distant colony male barks. The non-local stimulus on Beagle Island was Olive Island barks and both geographic distance and acoustic distance between these two colonies are large, and therefore, the strong discrimination can be explained on this basis. Similarly, Olive Island male responses can be explained by larger acoustic dissimilarity and long geographic distance between colonies.

For Liguanea and Lewis Island males, we had non-local barks from both nearby and distant colonies, but the results for these two colonies were quite different. On Liguanea Island males did not show any significant differences in their behavioral responses to barks from local, near (Lewis Island) or distant (Olive Island) colonies. Acoustically, Liguanea Island male barks are quite similar to both Lewis and Olive Islands male barks (acoustic distance 0.35 and 0.34, respectively) and this might explain why males showed low discrimination. Surprisingly though on Lewis Island, males' reactions to barks from Liguanea Island were significantly weaker than to local barks. Lewis males actually reacted as strongly to barks from the distant colony (Olive Island) as to local barks. Acoustically male barks are more similar between Lewis Is. and Liguanea Is. (0.34) than between Lewis Is. and Olive Is. (0.86). These results show that it is quite difficult to give a clear, uniform explanation for the observed differences in male responses to different non-local stimulus. Acoustic similarity/dissimilarity and geographic distance between colonies do not seem to be sufficient to fully explain observed vocal discrimination. Perhaps this is not surprising considering that variation in bark characteristics is related to geographic distance mostly only over large spatial scales, i.e., between Western Australia and South Australia (Ahonen et al. 2014). Possible explanations for the lack of vocal discrimination between different non-local colonies may be found from differences in the level of male movement between nearby colonies (Ahonen et al. 2016) or from different levels of male competition across colonies.

Biological meaning of vocal discrimination—implications for mating strategies

The ability of the Australian sea lion male to discriminate among locals using barks is consistent with findings from other bird and mammal species where individuals also respond more strongly to vocalizations of local individuals than those from non-local individuals (in birds: Brunton et al. 2008; Nelson and Soha 2004; Mortega et al. 2014; in mammals: Müller and Manser 2007; Charrier et al. 2013; Lin et al. 2016). Our results suggest that local individual males are a bigger threat in terms of mate competition and breeding success than are non-local ones. Although Australian sea lions breed asynchronously and have the capacity for long-distant dispersal, genetic evidence shows that males actually exhibit remarkably restricted dispersal (Ahonen et al. 2016). Moreover, this small-scale dispersal is supported by paternity analysis where local males secure the majority of matings (Ahonen 2014). This suggests that the chance of encountering reproductively active non-local males on a given breeding colony is quite low. Furthermore, in general pinnipeds are seasonally fertile (Atkinson and Gilmarti 1992; Atkinson 1997) and it is possible that these males may well be in their infertile phase given asynchrony of spermatogenesis, and thus, non-local males are not likely to represent a high threat level compared to local males. However, as Australian sea lions are non-annual and non-seasonal breeders it is not clear if the spermatogenesis is continuous or not in this species.

Given the potentially lower threat to reproductive success imposed by non-local males, the ability to discriminate could be maintained by a marginal gain, which we suggest might be energy conservation. Competition among males is exacerbated by the prolonged breeding season (McIntosh et al. 2012) and exceptionally low colony densities that result in relatively low numbers of receptive females present at any given time. This means each mating opportunity is valuable but dispersed. Mate-guarding, agonistic behavior and fight escalation all have potentially high costs, and mechanisms that avoid unnecessary expenditure, such as discriminating barks of non-local males and not wasting energy on nonessential agonistic behavior, could be maintained by even relatively marginal energy savings. Our findings provide insights into selection for competitors' discrimination using geographic variations in vocalizations. The ability to vocally discriminate serious rivals from potential but low threat rivals may have significant payoff in allocation of scarce resources to mate-guarding males.

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Compliance with ethical standards

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

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed. This research was approved by DEH SA Wildlife Ethics Committee (44/2008). Research on these islands was conducted under permission obtained from the Department of Environment, Water and Natural Resources, South Australia (permit Z25675) and the Department of Environment and Conservation, Western Australia (DEC WA License SF007255 and SF008193).

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