



**HAL**  
open science

## Good fences make good neighbours: territorial male Cape fur seals use spatial acoustic map of neighbours

Mathilde Martin, Tess Gridley, Simon Harvey Elwen, I. Charrier

### ► To cite this version:

Mathilde Martin, Tess Gridley, Simon Harvey Elwen, I. Charrier. Good fences make good neighbours: territorial male Cape fur seals use spatial acoustic map of neighbours. *Behaviour*, 2023, 160 (6), pp.499-514. 10.1163/1568539X-bja10218 . hal-04207549

**HAL Id: hal-04207549**

**<https://hal.science/hal-04207549>**

Submitted on 10 Nov 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1

2

# **Good fences make good neighbours: Territorial male Cape fur**

3

## **seals use spatial acoustic map of neighbours**

4

5

6

### **Authors**

7

M. Martin<sup>1,2,\*</sup>; T. Gridley<sup>2,3</sup>; S.H. Elwen<sup>2,3</sup> & I. Charrier<sup>1</sup>

8

9

### **Affiliations**

10

<sup>1</sup>Université Paris-Saclay, CNRS, Institut des Neurosciences Paris-Saclay,

11

151 Route de la Rotonde, 91400, Saclay, France

12

13

<sup>2</sup>Sea Search Research and Conservation NPC,

14

4 Bath Road, Muizenberg, Cape Town, 7945, South-Africa

15

16

<sup>3</sup>Department of Botany and Zoology, Faculty of Science, Stellenbosch University,

17

Stellenbosch, 7605, South Africa.

---

\*Corresponding author's e-mail address: mathilde.martin@universite-paris-saclay.fr

18

## **Abstract**

19 In territorial species, individual recognition among neighbouring males is likely to reduce  
20 energy expenses and risk of injury associated with the costly period of maintaining territory  
21 during the breeding season. This study explored neighbour-stranger vocal recognition in male  
22 Cape fur seals, one of the most colonial and polygynous mammalian species. Playback  
23 experiments revealed that territorial males were able to recognise the calls of their neighbours,  
24 in combination with the relative spatial position of the neighbour to their own harem. No ‘dear-  
25 enemy’ nor ‘nasty neighbour’ effects were detected. However, the strongest responses observed  
26 were made towards the calls of familiar neighbours played back from an incongruent location,  
27 simulating a situation in which a neighbour is outside its own territory. The colony structure  
28 and movements of the seals across the day could explain such results. This study has  
29 implications for understanding how vocal signals regulate interactions among males in  
30 polygynous mammals, particularly during the competitive mating period.

31

32

33

## **Keywords**

34 Territorial defence, Dear-enemy effect, Neighbour, Stranger, Vocal communication, Recognition,

35

Playback experiments

## 36 **1. Introduction**

37 Polygynous breeding systems in which males typically breed with several females - while each  
38 female breeds with a single male- are very common among mammals (about 95% of the species,  
39 Kunz & Orrell, 2004). The broad continuum of polygyny can be subdivided into several types  
40 of strategies depending on what males compete for i.e. fixed space or specific resources, direct  
41 access to females, or both (Cézilly & Danchin, 2008). In harem-defence polygyny, males  
42 compete to achieve a position among females (Campagna, 2018). This breeding structure  
43 generally occurs in species with synchronous reproduction and gregarious females during the  
44 breeding season (Davies, Krebs, & West, 2012) with comparatively low cost and easy access  
45 to high-quality males for females. In contrast, this mating strategy is extremely energetically  
46 costly for males: their reproductive success depends entirely on their ability to acquire and  
47 maintain a harem throughout the breeding season. Indeed, males have limited access to food  
48 resources during the territory tenure period and engage in aggressive behaviours including  
49 physical fights with their rivals to occupy a territory, exclude potential intruders and herd  
50 females (Wilson, 2000).

51         One of the most effective ways to minimise energy expenditure and risk of injury during  
52 territory tenure is to reduce the number of hostile interactions, and in particular to avoid  
53 aggressive behaviours in low-threat situations. For a territorial male, a neighbour settled in an  
54 adjacent territory and monopolizing a group of females should be less threatening than a non-  
55 established or stranger male attempting to compete for his harem or engage in sneaky matings  
56 (i.e. mating with a female belonging to the harem of another male) (Ydenberg, Giraldeau, &  
57 Falls, 1988; Temeles, 1994). It is therefore more advantageous for a male to save his finite  
58 energy resources to fight against possible intruders compared to neighbour males that do not  
59 represent an immediate threat his territorial integrity. The phenomenon in which the response  
60 of a male to his neighbour is reduced compared to his response to a stranger is known as the

61 'dear-enemy effect' (Fisher, 1954). Simultaneously, this social organization leads to a  
62 cooperative system among neighbouring territorial males that tolerate each other's presence in  
63 close proximity (Lesbarrères & Lodé, 2002). They mutually benefit by minimising aggression  
64 and time spent patrolling. However, a neighbour male can become a serious threat if he breaks  
65 the agreement by attempting to steal resources (females) from an adjacent territory and/or  
66 expand his own territory to the detriment of his close neighbours (Trivers, 1971; Godard, 1993;  
67 Dalton et al., 2020). In case of no respect of the agreed-upon boundary, the two individuals  
68 become rivals and the deceived male will immediately challenge the intruder (Godard, 1993;  
69 Clutton-Brock & Parker, 1995).

70 In this context, being able to recognise neighbouring males during territory tenure is  
71 crucial for males and may provide a significant advantage to their reproductive success. Across  
72 species, the use of vocal signals plays a major role in individual recognition processes such as  
73 male-male recognition (Bradbury & Vehrencamp, 2011) and consequently, in the dear enemy  
74 effect (Temeles, 1994). Most studies that have examined neighbour-stranger vocal recognition  
75 between territorial males have focused on passerine (for review see Werba et al., 2022) and  
76 non-passerine birds (e.g. Radford, 2005; Hardouin, Tabel, & Bretagnolle, 2006; Mager,  
77 Walcott, & Piper, 2010), and to a lesser extent amphibians (e.g. Davis, 1987; Lesbarrères &  
78 Lodé, 2002; Tumulty & Bee, 2021). Surprisingly, a remarkably small number of studies have  
79 investigated this vocal discrimination in mammals, despite the high number of territorial species  
80 in this taxon. The dear-enemy effect based on vocal cues has only been reported so far in three  
81 mammal species: the Australian fur seal *Arctocephalus pusillus dorifus* (Tripovich et al.,  
82 2008), the Subantarctic fur seal *Arctocephalus tropicalis* (J.-P. Roux & Jouventin, 1987) and  
83 the hippopotamus *Hippopotamus amphibius* (Thévenet et al., 2022). Although tested, there was  
84 no difference in responses to vocal signal produced by neighbour or stranger individuals in  
85 North American red squirrels *Tamiasciurus hudsonicus* (Wilson et al., 2015) or the Collared

86 pika *Ochotona collaris* (Trefry & Hik, 2009). There is therefore a significant lack of knowledge  
87 on how territorial males modulate their interactions during the energetically demanding period  
88 of territory tenure and whether the dear enemy effect is widespread in mammals or restricted to  
89 certain taxa or breeding systems.

90         Here, we focused on the Cape fur seal, *Arctocephalus pusillus pusillus*, a species subject  
91 to strong ecological constraints during the breeding season. The Cape fur seal is one of the most  
92 colonial mammal species in the world with colonies of several hundreds of thousands of  
93 individuals forming during the breeding season (lasting from mid-November to early-January  
94 each year; Rand, 1955). Males are sexually mature around 5 years old (i.e. subadult males) but  
95 do not hold a harem before they reach the social maturity at 8 to 13 years (i.e. adult males;  
96 Jefferson, Webber, & Pitman, 2011). At the beginning of the breeding season, adult males  
97 compete for territories and establish harems of up to 30 females with their newborn pups  
98 (Wickens & York, 1997). As all fur seal species, territorial males do not go to sea and fast  
99 throughout their territory tenure and display aggressive behaviours towards other males, both  
100 adults and subadults (Riedman, 1990). In contrast to many fur seal species, Cape fur seal  
101 subadult males are highly abundant on breeding colonies and occur in close proximity to  
102 territorial males (Nowak & Walker, 2003). They alternate periods at sea (to thermoregulate or  
103 to feed) with periods in the colony to rest or look for mating opportunities at the edge of harems.  
104 Territorial males are therefore constantly challenged and spend their time patrolling their harem  
105 and confronting rivals. During territorial displays, adult males produce barks i.e. short calls  
106 (average duration of  $1.25 \pm 0.36$  s) always emitted in a sequence (Martin et al., 2021a) (Figure  
107 1). Bark sequences have an average duration of  $11.8 \pm 8.7$  s and the average fundamental  
108 frequency of bark units is  $124 \pm 28$  Hz (Martin et al., 2021a). Territorial males' barks are  
109 produced at an amplitude of  $84 \pm 2$  dB SPL at 1m (Martin et al., 2022). These vocalizations  
110 convey different types of information such as the individual identity of the caller (Martin et al.,

111 2021b) and its arousal state (Martin et al., 2022). Although barks contain identity information  
112 with acoustic features which may allow for individual recognition, no study has experimentally  
113 tested the use of such vocalisations for individual vocal recognition between neighbouring  
114 territorial males.

115 In this study, we investigated the neighbour-stranger vocal recognition in Cape fur seal  
116 territorial males and tested the occurrence of a ‘dear-enemy’ phenomenon in this species.  
117 Secondly, we evaluated the behavioural response of territorial males in  
118 experiments representing a neighbouring male which had moved outside its harem. The results  
119 of this study will increase our knowledge on how vocalisations regulate interactions among  
120 males in polygynous mammals, particularly during the competitive mating period.

121

122

## 123 **2. Material and methods**

### 124 *2.1 Study location and focal individuals*

125 The study was conducted at Pelican Point breeding colony (Walvis Bay, Namibia) in  
126 November-December 2019 and October-November 2021, over 14 trial days. The experiments  
127 started from the end of October to avoid the unstable period of harem establishment at the  
128 beginning of the breeding season. Only harems that appeared to be well established and stable  
129 were included in the study. They also had to be located at different places on the colony to avoid  
130 resampling.

131 Before each experiment, the territorial males' behaviour and associated harem structure  
132 was observed for at least 1 hour, to ensure good knowledge of the relative organization and to  
133 identify their stable neighbours as well as the spatial boundaries of harems in the focal area.

134 When territorial males were not marked using water-based paint, they were identified through  
135 their physical characteristics and natural markings (fur colour pattern and scars) and their  
136 vocalizations (barks are sufficiently distinctive to allow the experimenters to discriminate  
137 among few individuals). Bark recordings and playback experiments were conducted mainly  
138 consecutively on the same day and the animals were visually monitored throughout the period  
139 of playback tracks creation. If tested on a later day, we used photo-identification to recognize  
140 them.

### 141 *2.2 Bark recording and creation of playback tracks*

142 Territorial males' barks were recorded using a Sennheiser ME67 directional shotgun  
143 microphone (frequency range: 40-20 kHz, sensitivity: 50 mV/Pa  $\pm$  2.5 dB) using a 44,1 kHz  
144 sampling rate and connected to a two-channel NAGRA LB digital audio recorder. The  
145 recordings were made at a distance of 10 to 20 m (visual estimation) from the barking male,  
146 depending on access to the animals and weather-related acoustic recording possibilities (i.e.  
147 wind speed and direction). Males were recorded while producing spontaneous barks (Figure 1)  
148 to advertise their presence while herding females i.e. during low arousal state activities  
149 (Mathilde Martin et al., 2022).

150 (Figure 1 here)

151 Playback tracks were built and edited using Avisoft SAS LAB Pro (R. Specht, Avisoft  
152 Bioacoustics, Berlin, Germany). Each track consisted of three bouts of barking recorded from  
153 the same territorial male and spliced together with a separation of 3 s between bouts. Playback  
154 tracks had an average duration of  $18.5 \pm 2.9$  s. Tracks were high-pass filtered at 100 Hz to  
155 remove most of the background wind and ocean noise. The exposure of a focal male to a three-  
156 bouts playback track constituted a playback series.

### 157 *2.3 Playback procedure*



158 Each focal individual was exposed to three different series which each had a different  
159 combination of playback track and loudspeaker location. In the control series, we simulated a  
160 case where the neighbour male produces barks from the location of his own harem (i.e. a  
161 familiar stimuli). Here barks recorded from the focal males' adjacent neighbour were played  
162 back by placing the speaker on the congruent side i.e. between the harem of the focal male and  
163 the harem of the broadcast neighbour male. The second type of series simulated a case where  
164 the neighbouring male has left his own harem and is barking from a novel location. For this,  
165 the same neighbour bark stimulus was broadcast from the opposite side (incongruent side) of  
166 the focal male's territory. The harem of the tested male was thus located between the  
167 loudspeaker and the harem of the neighbour male. Finally, the third type of series aimed to test  
168 differences between the simulated neighbour vocalising from a novel location and a stranger.  
169 'Stranger' barks were recorded from males that held harems outside the study area. We  
170 attempted to reduce the likelihood of familiarity by recording stranger males located between  
171 100 m and 1 km away from the study area and tested males. Series of 'stranger' barks were  
172 broadcast from the incongruent side. Focal males were exposed to the three series within the  
173 same day and two successive series were separated by at least 10 minutes or until the focal male  
174 remained to a baseline behaviour (i.e., laying down or standing still, and not interacting with  
175 another individual). The order of series presentation was randomised for each focal male.

176 First, the speaker was moved close to the focal male using a 5-m pole (to minimise  
177 disturbance induced by the presence of the experimenters) to be within a distance of 8 to 15 m  
178 depending on harem size and thus territory size. The speaker was always placed at the  
179 boundaries of the territory as ascertained by pre-recording observations. Once the speaker was  
180 settled, we waited for the focal individual to be either laying down or standing still, and not  
181 interacting with another individual. Then, playback tracks were broadcasted using a waterproof  
182 and wireless high-powered speaker (JBL Charge 3, 2 x 10 W, frequency response: 65 Hz – 20

183 kHz) connected to a Bluetooth sound player (Sony NW-A35). The amplitude level of the  
184 playback tracks was adjusted to the natural amplitude of male barks at the range of 8 to 15m  
185 ( $84 \pm 2$  dB SPL at 1 m, measured with a 'Testo 815' sound level meter, A-weighting, fast-  
186 response (Mathilde Martin et al., 2022). Playback experiments were filmed using a Fujifilm  
187 FinePix XP90 or an Olympus Tough TG-6 camera to allow further analysis.

#### 188 *2.4 Behavioural response*

189 The behavioural response of the focal individual was examined from video footage for 30 s  
190 from the start of the playback. Response variables were latency to look towards the speaker (all  
191 latency measures in seconds), look duration towards the speaker, latency to bark in response,  
192 barking duration (s) and latency to posture change (the individual changed from lying down to  
193 standing or from standing still to moving). An absence of a given behaviour (look, barking,  
194 posture change) was assigned a default value of 30 s for latencies.

#### 195 *2.5 Statistical analysis*

196 A principal component analysis (PCA) was performed on the five behavioural variables to  
197 combine them into a score representing the general behavioural response of the focal individual  
198 during a playback series. Only principal components (PC) with eigenvalues greater than 1 were  
199 retained. PC scores were compared between the three types of playback series using a linear  
200 mixed-effects model (LME) performed with the *lme4* R package (Bates et al., 2015). The focal  
201 male's identity was set as a random effect to account for the fact that the data are non-  
202 independent (three series were conducted on the same individual). A pairwise analysis of  
203 estimated marginal means (EMM) was conducted using the *emmeans* R package (Lenth, 2021).  
204 It included a Holm-Bonferroni correction for multiple comparisons. Finally, a linear model  
205 (LM) was fitted to test the effect of the order of broadcast of three stimuli on the behavioural  
206 response of the focal individual.

207

### 208 3. Results

209 A total of 19 territorial males (8 in 2019 and 11 in 2021) were exposed to the three stimuli  
210 types: ‘neighbour’, ‘neighbour from the opposite side’ and ‘stranger’. Values of the five  
211 response variables measured during the playback series are presented in Figure 2. The PCA  
212 extracted five principal components but only PC1 and PC2 had an eigenvalue greater than 1  
213 (2.57 and 1.27 respectively) and were thus retained for further analysis. They explained 76.78%  
214 of the total variance. PC1 was highly correlated with all five variables (Table 1), thereby  
215 representing the general behavioural response (look, barks, posture change) of the focal male.

	PC1	PC2
Eigenvalues	2.57	1.27
% cumulative variance	51.33	76.78
Correlation coefficients between PC and variables		
Latency to look	<b>0.64</b>	<b>-0.61</b>
Look duration	<b>-0.69</b>	<b>0.61</b>
Latency to bark	<b>0.82</b>	0.40
Barking duration	<b>-0.60</b>	-0.58
Latency to posture change	<b>0.81</b>	0.18

216 Table 1: Summary of the first two principal components (PC1 and PC2) resulting from the principal  
217 component analysis (PCA) performed with the five behavioural variables

218

219 Negative values of PC1 scores corresponded to short latencies to look towards the speaker, to  
220 bark and to change posture. They also matched with a long period of looking towards the  
221 speaker and long period of barking. The strength of the behavioural response of the tested males  
222 was therefore inversely proportional to the PC1 scores. PC2 explained less variance compared  
223 to PC1 and was mainly correlated with the variables related to looking towards the speaker  
224 (Table 1). Since the look variables were already highly correlated to PC1, it seemed that the  
225 behavioural response of the tested males could be reasonably estimated by taking into account  
226 only PC1.

227 (Figure 2 here)

228 Significant differences in PC1 scores i.e. in males' behavioural response to playbacks series  
229 were found between the three types of stimuli (LME:  $F = 6.717$ ,  $df = 2$ ,  $p = 0.0033$ ). The general  
230 response of males to their neighbour's vocalisations was higher when barks were broadcasted  
231 from the incongruent location compared to the congruent location (EMM: estimate = 1.631, SE  
232 (standard error) = 0.468,  $df = 36$ ,  $t$ -ratio = 3.488 and  $p = 0.0039$ ; Figure 3). Furthermore, the  
233 response to a neighbour in a novel location was stronger than to a stranger male in the same  
234 location (EMM: estimate = -1.272, SE = 0.468,  $df = 36$ ,  $t$ -ratio = -2.719 and  $p = 0.02$ ; Figure  
235 3). No differences in males' response was found between the neighbour from the congruent  
236 location and stranger playbacks (EMM: estimate = 0.359, SE = 0.468,  $df = 36$ ,  $t$ -ratio = 0.769  
237 and  $p = 0.4471$ ; Figure 3). No differences in PC2 scores were reported between the three stimuli  
238 (LME:  $F = 1.4335$ ,  $df = 2$ ,  $p = 0.2518$ ).

239 (Figure 3 here)

240 The order of broadcast of the three stimuli did not influence the behavioural response of the  
241 focal male (LM:  $F = 0.3843$ ,  $df = 2$ ,  $p = 0.6828$ ) demonstrating the order of stimuli presentation  
242 did not bias these results.

243

#### 244 4. Discussion

245 In species exchanging vocal signals to modulate interactions among territorial males during the  
246 breeding season, the dear-enemy-effect is characterized by a reduced response to calls produced  
247 by a neighbouring male compared to calls from a stranger one. This phenomenon is well known  
248 and widespread within bird species (for review see Werba et al., 2022), but is poorly studied in  
249 mammals (J. P. Roux & Jouventin, 1987; Tripovich et al., 2008; Trefry & Hik, 2009; D. R.  
250 Wilson et al., 2015; Thévenet et al., 2022). Our results revealed that territorial Cape fur seal

251 males responded more strongly to their neighbour's bark broadcasted from an incongruent  
252 location than to a stranger territorial male's bark broadcasted from the same location. Their  
253 behavioural response was characterised by a significant increase in all vigilance behaviours  
254 towards the noise source i.e. looking towards the speaker, moving from a lying to a sitting  
255 position to observe the situation and producing barks that advertise its presence and challenge  
256 the intruder. These findings highlight that territorial males are able to individually recognise  
257 barks of neighbouring males and memorize the spatial location of the territory and males around  
258 their harem. If territorial males could not recognise their neighbour's vocalisations, then all  
259 playback trials performed from the incongruent location would induce the same degree of  
260 behavioural response. Here, the tested males were significantly more vigilant during their  
261 neighbour's barks broadcast from the incongruent direction, indicating that they distinguished  
262 these vocalisations from those of a stranger male, and that they were aware of the expected  
263 location and movement of their neighbour into an unusual location.

264         The use of barks for individual vocal recognition among males was shown in two other  
265 fur seal species (J. P. Roux & Jouventin, 1987; Tripovich et al., 2008) but this study is the first  
266 to provide evidence of their ability to associate a vocal signal with a specific spatial location.  
267 Cape fur seal males' barks show a high degree of individual vocal stereotypy (Mathilde Martin  
268 et al., 2021b). It is likely that territorial males can detect inter-individual variations in the  
269 acoustic features of barks thus learning the characteristics of their neighbours' voices. This  
270 individual recognition would make it possible to modulate interactions between neighbouring  
271 males, in order to establish a system of tolerance allowing each of them to reduce the risks (loss  
272 of energy, injuries) associated with aggressive behaviour during the breeding period. This is  
273 particularly advantageous in species such as pinnipeds in which territorial males fast for the  
274 duration of their territory tenure. From the perspective of information encoding, it would be  
275 interesting to study which acoustic features are involved in the male-male recognition system.

276 We hypothesize that the fundamental frequency, duration of the barks and bark rate play an  
277 important role in this cognitive process as these are highly individualized acoustic features in  
278 Cape fur seal males' barks (Mathilde Martin et al., 2021b).

279 Our results showed that territorial males are able to recognise the voices of neighbouring  
280 males, providing the basis for the establishment of the dear-enemy effect. However, no evidence  
281 of this effect was found. Indeed, in our experiments, territorial males displayed the same  
282 behavioural response (i.e., weak reaction) whether they were exposed to barks from a neighbour  
283 (broadcasted from the neighbour male's territory) or to barks from a stranger male. It appears  
284 that strangers were regarded as a similar level of threat to a familiar neighbour in his territory.  
285 These results are strongly discordant with the dear-enemy hypothesis stating that males use  
286 vocal recognition of neighbours to restrict their aggressive behaviour towards strangers (Fisher,  
287 1954). It is inconsistent with other investigations on fur seals (J. P. Roux & Jouventin, 1987;  
288 Tripovich et al., 2008) but the absence of a dear-enemy effect is not an isolated case as it has  
289 been reported in other mammal species (Trefry & Hik, 2009; D. R. Wilson et al., 2015). We  
290 believe that a similar response to a neighbour (in his territory) or an unfamiliar male may be  
291 due to the high density of males present in colonies (at least in our study site, Pelican Point).  
292 Indeed, contrary to other fur seal species in which subadult males (i.e., socially immature males)  
293 do not haul-out in breeding colonies, there is a high number of subadults roaming at Pelican  
294 Point. These young individuals can lead to a slight decrease in the reproductive success of  
295 territorial males in cases of sporadic successful mating with a female, but do not represent a  
296 strong threat to the integrity of the territory, as they do not significantly challenge territorial  
297 males (Martin, pers. obs.). We suggest that the approach of a stranger male would be considered  
298 as a low threat for a territorial male, given the high probability that it is a roaming subadult.  
299 This may explain why the response of territorial males to the vocalizations of a stranger male  
300 is relatively low. The present findings cannot be either explained by the 'nasty neighbour'

301 phenomenon (Temeles, 1994; Müller & Manser, 2007; Carazo, Font, & Desfilis, 2008). In the  
302 latter, there is an increased aggressiveness of males towards neighbours than towards strangers.  
303 But here, responses to neighbour at the congruent location were not stronger than those to a  
304 stranger.

305         The strongest responses observed in this study were made towards the calls of adjacent  
306 neighbours from incongruent locations, simulating a situation in which a neighbour is outside  
307 its own territory. When hearing a neighbour male barking from an incongruent location, tested  
308 males were more alert as they looked towards the speaker more quickly and for longer durations  
309 compared to when exposed to neighbour's barks from a congruent location. In addition, some  
310 males showed stronger signs of aggressiveness such as the production of barks or the transition  
311 from laying down or standing still to moving towards the sound source for series broadcasted  
312 from the incongruent side. In this species, individual vocal recognition of neighbouring males  
313 would rather serve to modulate interactions between neighbours than between neighbours and  
314 strangers. We suggest that the density of males in the colony could also be an explanation.  
315 While territorial males are not always aware of the status of stranger males, they know that their  
316 adjacent neighbours are territorial, socially mature and actively seeking breeding opportunities,  
317 thus posing a real threat to their reproductive success. Therefore, when a neighbouring male  
318 known to hold a harem is exploring new areas, he might be perceived to be targeting the focal  
319 male's territory or steal females or mating opportunities. Thus, the threat is perceived as  
320 significant and the reaction must be immediate. In accordance with Muller & Manser (2007),  
321 we suggest that the level of competition among territorial males and the group density, could  
322 positively affect the occurrence of this effect in social species.

323         To conclude, this study provided the first evidence of spatial acoustic map of neighbours  
324 in Cape fur seal territorial males during the breeding season. By conveying information about  
325 the identity of the emitter, barks allow significant modulation of social interactions between

326 territorial males during the challenging and energy-consuming period. The structure of the  
327 colony (high number of roaming subadult males near harems) and the movements of animals  
328 across the day (short swims to thermoregulate, tide patterns) may lead to an increased vigilance  
329 of territorial males towards their neighbours as these ones might be willing to expand their own  
330 territory and thus steal females compared to stranger males (likely subadult males), which do  
331 not seem to represent a strong threat for their breeding success.

332

### 333 **Figure Captions**

334 **Figure 1:** Spectrogram of a Cape fur seal adult male bark generated using Seewave  
335 (Sueur, Aubin, & Simonis, 2008) (Hamming window size: 1024 pts, 90% overlap).

336 **Figure 2:** Response variables measured during the playback trials conducted on  
337 territorial males (n=19) exposed to three different stimuli: a, Latency to look (in sec); b, Look  
338 duration (in sec); c, Latency to bark (in sec); d, Barking duration (in sec); e, Latency to posture  
339 change (in sec). *Boxplots present median values with first and third quartiles (lower and upper*  
340 *hinges) and the interval between the smallest and the largest values (whiskers, no further than*  
341 *1.5\*IQR from the hinge). Diamonds represent mean values.*

342 **Figure 3:** Strength of the behavioural response (indicated by PC1 scores) of territorial  
343 males (n=19) to the three different stimuli. *Y axis is reversed because highly negative*  
344 *PC1 scores values correspond to a strong behavioural response. Boxplots present median*  
345 *values with first and third quartiles (lower and upper hinges) and the interval between the*  
346 *smallest and the largest values (whiskers, no further than 1.5\*IQR from the hinge). Diamonds*  
347 *represent mean values. Statistical test: linear mixed-effects model supplemented with a*  
348 *pairwise analysis of estimated marginal means. (Significance code: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*'*  
349 *0.05 'NS: not significant' 1).*



350

351 **Acknowledgements**

352 We acknowledge the Namibian Ministry of Fisheries and Marine Resources and the Namibian  
353 Chamber of Environment for their support on this research. We thank Dorothy Fourie and  
354 Antonia Immerz for their help with data collection. We thank Naude Dreyer and the Ocean  
355 Conservation Namibia team for their logistical support and their enthusiasm for the project.  
356 Experiments were approved by the Research Ethics Committee (Animal Care and Use) of  
357 Stellenbosch University and authorized by the Namibian National Commission on Research  
358 Science and Technology (NCRST; Authorization No: AN202101095).

359

360 **References**

- 361 Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects  
362 Models Using lme4– J. Stat. Softw. 67: 1–48.
- 363 Bradbury, J.W. & Vehrencamp, S.L. (2011). Principles of Animal Communication. Sinauer  
364 Associates, Inc.
- 365 Campagna, C. (2018). Aggressive Behavior, Intraspecific– In: Encycl. Mar. Mamm. (Third  
366 Ed. (Bernd, W., Thewissen, J.G.M., & Kovacs, K.M., eds). Elsevier Inc., p. 15–20.
- 367 Carazo, P., Font, E., & Desfilis, E. (2008). Beyond “nasty neighbours” and “dear enemies”?  
368 Individual recognition by scent marks in a lizard (*Podarcis hispanica*)– Anim. Behav. 76:  
369 1953–1963.
- 370 Cézilly, F. & Danchin, E. (2008). Mating systems and parental care– In: Behav. Ecol.  
371 (Danchin, E., Giraldeau, L.A., & Cézilly, F., eds). New York, Oxford Uni., p. 429–465.
- 372 Clutton-Brock, T.H. & Parker, G.A. (1995). Punishment in animal societies– Nature 373:  
373 209–216.
- 374 Dalton, B., Settle, R., Medley, K., & Mathis, A. (2020). When neighbors cheat: a test of the  
375 dear enemy phenomenon in southern red-backed salamanders– Behav. Ecol. Sociobiol.

376 74.

377 Davies, N.B., Krebs, J.R., & West, S.A. (2012). An introduction to behavioural ecology, John  
378 Wiley.

379 Davis, M.S. (1987). Acoustically mediated neighbor recognition in the North American  
380 bullfrog, *Rana catesbeiana*– Behav. Ecol. Sociobiol. 21: 185–190.

381 Fisher, J.B. (1954). Evolution and bird sociality– In: Evol. as a Process (Huxley, J., Hardy,  
382 A.C., & Ford, E.B., eds), p. 71–83.

383 Godard, R. (1993). Tit for tat among neighboring hooded warblers– Behav. Ecol. Sociobiol.  
384 33: 45–50.

385 Hardouin, L.A., Tabel, P., & Bretagnolle, V. (2006). Neighbour-stranger discrimination in the  
386 little owl, *Athene noctua*– Anim. Behav. 72: 105–112.

387 Jefferson, T.A., Webber, M.A., & Pitman, R.L. (2011). Marine mammals of the world: a  
388 comprehensive guide to their identification, Elsevier.

389 Kunz, T.H. & Orrell, K.S. (2004). Reproduction, Energy Costs of– In: Encycl. Energy.  
390 Elsevier, p. 423–442.

391 Lenth, R. V. (2021). emmeans: Estimated Marginal Means, aka Least-Squares Means. R  
392 package version 1.6.2-1.

393 Lesbarrères, D. & Lodé, T. (2002). Variations in male calls and responses to an unfamiliar  
394 advertisement call in a territorial breeding anuran, rana dalmatina: Evidence for a “dear  
395 enemy” effect– Ethol. Ecol. Evol. 14: 287–295.

396 Mager, J.N., Walcott, C., & Piper, W.H. (2010). Common Loons can differentiate yodels of  
397 neighboring and non-neighboring conspecifics– J. F. Ornithol. 81: 392–401.

398 Martin, M., Gridley, T., Elwen, S.H., & Charrier, I. (2022). Feel the beat: cape fur seal males  
399 encode their arousal state in their bark rate– Sci. Nat. 109.

400 Martin, Mathilde, Gridley, T., Elwen, S., & Charrier, I. (2021a). Vocal repertoire , micro-  
401 geographical variation and within-species acoustic partitioning in a highly colonial  
402 pinniped, the Cape fur seal– R. Soc. Open Sci. 8: 1–18.

403 Martin, Mathilde, Gridley, T., Elwen, S., & Charrier, I. (2021b). Extreme ecological  
404 constraints lead to high degree of individual stereotypy in the vocal repertoire of the

405 Cape fur seal (*Arctocephalus pusillus pusillus*)– Behav. Ecol. Sociobiol. 75: 1–16.

406 Martin, Mathilde, Gridley, T., Elwen, S.H., & Charrier, I. (2022). Feel the beat: cape fur seal  
407 males encode their arousal state in their bark rate– Sci. Nat. 109: 1–11.

408 Müller, C.A. & Manser, M.B. (2007). “Nasty neighbours” rather than “dear enemies” in a  
409 social carnivore– Proc. R. Soc. B Biol. Sci. 274: 959–965.

410 Nowak, R. & Walker, E. (2003). Walker’s marine mammals of the world, JHU Press.

411 Radford, A.N. (2005). Group-specific vocal signatures and neighbour-stranger discrimination  
412 in the cooperatively breeding green woodhoopoe– Anim. Behav. 70: 1227–1234.

413 Rand, R.W. (1955). Reproduction in the female Cape Fur Seal, *Arctocephalus pusillus*  
414 (Schreber)– Proc. Zool. Soc. London 124: 717–740.

415 Riedman, M. (1990). The pinnipeds: seals, sea lions, and walruses. Univ of California Press,  
416 (Vol. 12).

417 Roux, J.-P. & Jouventin, P. (1987). Behavioral Cues to Individual Recognition in the  
418 Subantarctic Fur Seal , *Arctocephalus tropicalis*.

419 Roux, J.P. & Jouventin, P. (1987). Behavioral Cues to Individual Recognition in the  
420 Subantarctic Fur Seal, *Arctocephalus tropicalis* (NOAA Tech. Rep. NMFS).

421 Sueur, J., Aubin, T., & Simonis, C. (2008). Seewave, a free modular tool for sound snalysis  
422 and synthesis– Bioacoustics 18: 213–226.

423 Temeles, E.J. (1994). The role of neighbours in territorial systems: When are they “dear  
424 enemies”?– Anim. Behav. 47: 339–350.

425 Thévenet, J., Grimault, N., Fonseca, P., & Mathevon, N. (2022). Voice-mediated interactions  
426 in a megaherbivore– Curr. Biol. 32: 70–71.

427 Trefry, S.A. & Hik, D.S. (2009). Eavesdropping on the neighbourhood: Collared pika  
428 (*Ochotona collaris*) responses to playback calls of conspecifics and heterospecifics–  
429 Ethology 115: 928–938.

430 Tripovich, J.S., Charrier, I., Rogers, T.L., Canfield, R., & Arnould, J.P.Y. (2008). Who goes  
431 there? Differential responses to neighbor and stranger vocalizations in male Australian  
432 fur seals– Mar. Mammal Sci. 24: 941–948.

- 433 Trivers, R.L. (1971). The Evolution of Reciprocal Altruism– *Q. Rev. Biol.* 41: 35–57.
- 434 Tumulty, J.P. & Bee, M.A. (2021). Ecological and social drivers of neighbor recognition and  
435 the dear enemy effect in a poison frog– *Behav. Ecol.* 32: 138–150.
- 436 Werba, J.A., Mm Stuckert, A., Edwards, M., & Mccoy, M.W. (2022). Stranger danger: A  
437 meta-analysis of the dear enemy hypothesis– *Behav. Processes* 194.
- 438 Wickens, P. & York, A.E. (1997). Comparative population dynamics of fur seals– *Mar.*  
439 *Mammal Sci.* 13: 241–292.
- 440 Wilson, D.R., Goble, A.R., Boutin, S., Humphries, M.M., Coltman, D.W., Gorrell, J.C.,  
441 Shonfield, J., & McAdam, A.G. (2015). Red squirrels use territorial vocalizations for kin  
442 discrimination– *Anim. Behav.* 107: 79–85.
- 443 Wilson, E.O. (2000). *Sociobiology: The New Synthesis*. Harvard University Press.
- 444 Ydenberg, R.C., Giraldeau, L.A., & Falls, J.B. (1988). Neighbours, strangers, and the  
445 asymmetric war of attrition– *Anim. Behav.* 36: 343–347.
- 446