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

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

Authors

M. Martin^{1,2,*}; T. Gridley^{2,3}; S.H. Elwen^{2,3} & I. Charrier¹

Affiliations

¹Université Paris-Saclay, CNRS, Institut des Neurosciences Paris-Saclay,
151 Route de la Rotonde, 91400, Saclay, France

²Sea Search Research and Conservation NPC,
4 Bath Road, Muizenberg, Cape Town, 7945, South-Africa

³Department of Botany and Zoology, Faculty of Science, Stellenbosch University,
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.

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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 ± 0.36 s) always emitted in a sequence (Martin et al., 2021a) (Figure
107 1). Bark sequences have an average duration of 11.8 ± 8.7 s and the average fundamental
108 frequency of bark units is 124 ± 28 Hz (Martin et al., 2021a). Territorial males' barks are
109 produced at an amplitude of 84 ± 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 ± 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 ± 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	0.64	-0.61
Look duration	-0.69	0.61
Latency to bark	0.82	0.40
Barking duration	-0.60	-0.58
Latency to posture change	0.81	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

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359

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