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Feel the beat: cape fur seal males encode their arousal state in their bark rate

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4 **Feel the beat: Cape fur seal males encode their arousal**
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7 **state in their bark rate**
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Abstract

1
2 The Cape fur seal is one of the most colonial mammal species in the world. Breeding colonies
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4 are composed of harems held by mature males (older than 10 years) with up to 30 females and
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6 their pups, while roaming subadult males (younger and socially immature) are kept away from
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8 bulls' territories. As in other pinnipeds, Cape fur seals are highly vocal and use acoustic signals
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10 in all their social interactions. Both sexes frequently produce barks - short vocalizations always
11
12 produced in sequences. Barks are produced by males for territorial defence, mating behaviours
13
14 and agonistic interactions and they convey information about the sex, age-class and individual
15
16 identity. This study investigated whether motivational cues such as the arousal state can be
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18 encoded in territorial males' barks and whether these cues are decoded by listening sub-adult
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20 males. The rate (number of calls per unit of time) and fundamental frequency of barks were
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22 found to significantly increase during high arousal state interactions (i.e. male-male
23
24 confrontation) compared to spontaneous barks. Playback experiments revealed that subadult
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26 males responded with a higher level of vigilance when territorial males' barks had a faster bark
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28 rate. This mechanism of decoding the bulls' arousal state from barks will likely constitute an
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30 advantage for both bulls and the subadult males, by avoiding or reducing physical conflicts, and
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32 thereby reducing energy expenditure and the risk of injury. This study is the first experimental
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34 evidence of Cape fur seals' ability to use rhythm in their vocalizations to modulate their social
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36 interactions.
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Keywords

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49 Cape fur seal; vocal communication; territorial defence; arousal state; rhythm perception
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Declarations

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Code availability: Not applicable.

Authors' contributions: I.C and M.M designed the study. I.C, T.G and S.H.E organised the fieldwork logistics. M.M and I.C collected the data. M.M analysed the data. M.M and I. C drafted the manuscript, and all authors revised the manuscript.

Ethics approval: This present study complies with the European Union Directive on the Protection of Animals Used for Scientific Purposes (EU Directive 2010/63/EU) and with current Namibian laws. Fieldwork was permitted by the Namibian Ministry of Fisheries and Marine Resources (MFMR).

Consent to participate: All authors consent to participate.

Consent for publication: All authors consent to publish this study.

Introduction

The use of acoustic signals for communication is widespread in animals, particularly in birds and mammals. Acoustic communication is involved in most social interactions including sexual interactions, parent-offspring relationships, territory defence, group coordination, and foraging (Halliday and Slater 1983). Acoustic signals can convey multiple types of information depending on their function and acoustic characteristics. Acoustic signals produced only in specific contexts become linked to a specific signal function and thus can provide information about their general environment. For example, the presence of predators can be advertised through alarm calls (Seyfarth et al. 1980; Blumstein and Armitage 1997a; Macedonia and Evans 2010; Moran 2010) or detection of food through species specific foraging calls (Chapman and Lefebvre 1990; Brown et al. 1991; Hauser et al. 1993; Mahurin and Freeberg 2009). Some vocalisations can give information about the emitter's social intentions linked to agonistic or affiliative interactions such as aggression or courtship calls (Owen et al. 2006; Charlton et al. 2007; Ballentine et al. 2008; Faragó et al. 2010). On a secondary level, vocalisations are further shaped by anatomo-morphological differences among individuals such as the size and shape of the body and/or the vocal tract which affect the voice of an animal, more formally referred to as 'source-filter theory' (Fant 1960; Taylor and Reby 2010). These variations can encode information about the emitter's species, sex, social rank, age, body size or individual identity and has been reported in many species (e.g. Charrier et al. 2001; Rendall 2003; Reby et al. 2005; Gwilliam et al. 2008; Briefer and McElligott 2011; Matrosova et al. 2011; Déaux et al. 2016). These acoustic 'voice' features constitute the 'static' component of the information encoded in signals (Taylor et al. 2016). This plays a major role in social interactions such as parent-offspring individual recognition, sexual competition, territoriality and mate selection (Bradbury and Vehrencamp 2011).

25 Acoustic signals can also convey information on the motivational and emotional state
26 of the emitter, called the ‘dynamic’ component (Ohala 1984; Taylor et al. 2016). The expression
27 of emotions in signals enhances the quantity of information transmitted as it provides additional
28 cues about the internal state of the calling individual or the urgency of the situation (Briefer
29 2020). Numerous studies have shown that vocalisations produced by mammals are capable of
30 expressing emotions (for review see Briefer 2012). The expression of emotional state in
31 communicative signals benefits both the transmitter and the receiver by reducing uncertainty
32 and eliciting appropriate behavioural responses (e.g. approach or avoidance), a crucial aspect
33 for an organism’s fitness (Dall et al. 2005). Conveying accurate emotional information through
34 acoustic signals can be especially advantageous in specific situations involving potentially high
35 energy expenditure such as predator avoidance or the assessment of rivals (Charrier et al. 2011;
36 Casey et al. 2015) and the general mediation of social interactions among individuals (Bradley
37 and Mennill 2009; Bradbury and Vehrencamp 2011; Brudzynski 2014; Papale et al. 2020).
38 Generally, the acoustic parameters mostly altered by arousal state are linked to the fundamental
39 frequency or energy distribution in the spectrum, and the temporal patterning of calls (number
40 of vocalizations/elements produced per unit of time and/or interval between those elements,
41 Briefer 2012). These dynamic variations in vocalizations are mostly involuntary, resulting from
42 changes in the somatic and autonomic nervous system which in turn lead to modifications in
43 vocal production organs as well as in respiration and salivation (Scherer 2003). Changes in the
44 call production rate within sequences have been reported to convey emotional or motivational
45 cues in signals of different species: non-song birds (Gemard 2020), songbirds (DuBois et al.
46 2009; Geberzahn and Aubin 2014) and multiple mammal species e.g. dogs (Yin and McCowan
47 2004), baboons (Rendall 2003), bats (Bastian and Schmidt 2008), marmots (Blumstein and
48 Armitage 1997b), mongoose (Manser 2001).

49 Due to the diversity of their social organizations and mating strategies, Otariid species
1
2 50 are a good model system in which to study vocal signals across a range of behavioural, mating
3
4 51 and ecological contexts. By being the most colonial pinniped species and with its complex
5
6 52 social organisation, the Cape fur seal (*Arctocephalus pusillus pusillus*) lie at one end of this
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8 53 spectrum. The investigation of emotional information encoded in males' vocalizations is
9
10 54 particularly interesting in this species for two reasons. First, this is a highly polygynous species
11
12 55 with territorial males competing for territories and constituting harems of up to 30 females with
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14 56 their pups (Wickens and York 1997). Harems are held by bulls whose age gives them sexual
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16 57 and social maturity: males become sexually mature at around 5 years (i.e. subadults), but they
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18 58 only reach the social maturity when they are 8 to 13 years old (i.e. adult or territorial males)
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20 59 (Jefferson et al. 2011). Adult males are much larger than subadult males, and show
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22 60 characteristic physical features: enlarged neck and shoulders, mane with longer guard hair
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24 61 around the neck and shoulders (Jefferson et al. 2011). In general, territorial males fast
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26 62 throughout the breeding period and display aggressive behaviours toward other territorial bulls
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28 63 or subadult males (Riedman 1990). In this context, the ability of animals to correctly identify
29
30 64 individual identity cues and emotional state are of great importance (Insley et al. 2003) for
31
32 65 males to be able to differentiate neighbouring territorial bulls from unfamiliar individuals, as
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34 66 well their arousal state in order to avoid unnecessary conflicts (Roux and Jouventin 1987;
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36 67 Tripovich et al. 2008b, c).
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69 Secondly, Cape fur seal subadult males are highly abundant on breeding colonies and
70 occur in close proximity to territorial males. It contrasts with most fur seal species for which
71 non-territorial males (subadults) do not haul-out on breeding colonies but form isolated groups
72 of immature individuals (Bartholomew 1959; Trillmich and Majluf 1981). Cape fur seal
73 subadult males are chased and kept out of harems by territorial males through aggressive

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74 behaviour and vocalizations. Subadults are quite mobile and roam over the entire colony: they
75 alternate resting periods in the colony with periods at sea to thermoregulate or to feed (unlike
76 territorial males that fast during the breeding season) (Nowak and Walker 2003). For subadult
77 males looking for mating opportunities at the edge of harems, the arousal state and behavioural
78 intentions of territorial bulls are important cues to decipher in order to adjust both their level of
79 vigilance and their behavioural response (e.g. escape in case of attack) (Jefferson et al. 2011).
80
81 This study aims to explore whether Cape fur seal males use acoustic signals to convey their
82 emotional state and to modulate social interactions during the breeding season. Cape fur seal
83 males produce barks in across a wide range of social interactions: from affiliative (mating
84 behaviours, adult males only) to agonistic, including both territorial defence (adult males only)
85 and general aggression (both adults and subadults) (Martin et al. *in revision*). Barks are very
86 short calls (mean duration: 0.12 s; Martin et al. *in revision*) always produced in sequences.
87 These vocalisations convey information about the sex and the age-class of the caller (Martin et
88 al. *in revision*), as well as individual identity (Martin et al. 2021). Individual identity is encoded
89 in both the frequency parameters of barks (the fundamental frequency and the energy
90 distribution among the spectrum) but also in temporal parameters relative to the sequences
91 (Martin et al. 2021). Temporal features in call sequences including the duration of a sequence,
92 the interval between barks or the bark rate has been shown to vary with behavioural context and
93 arousal state of males in several otariid species including three species of sea lion species
94 (Peterson and Bartholomew 1969; Schusterman 1977; Fernández-Juricic et al. 2001; Kunc and
95 Wolf 2008). In fur seals, it has been suggested in Subantarctic fur seal (Roux 1986) but
96 empirically tested for only one species, the Australian fur seal (Tripovich et al. 2008a).

97 The aim of this study was twofold. We first investigated if the acoustic characteristics
98 of Cape fur seal territorial males' barks change with the behavioural context and their arousal
99 state. We hypothesized that the bark rate could be involved in this process, with high arousal

100 states inducing an increase in bark rate, but we explored this hypothesis using multiple acoustic
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2 101 parameters of barks. Secondly, playback experiments were performed on subadult males to
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4 102 investigate if their behavioural response varies with the acoustic features of barks produced by
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7 103 a territorial male. Unlike territorial males that have established territories and are likely able to
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9 104 recognize each other by their vocalizations (demonstrated in several pinniped species: Gwilliam
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11 et al. 2008; Tripovich et al. 2008; Casey et al. 2015), roaming subadults may be unfamiliar to
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14 106 the barks of surrounding territorial males when they temporarily rest in one place. Therefore,
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17 107 we hypothesised that subadult males may use information encoded in acoustic signals to assess
18
19 108 the general arousal state of nearby territorial males and thus determine their threat level. This
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22 109 is the first study to experimentally investigate the mechanisms of coding-decoding the arousal
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24 110 state in vocal signals between territorial and subadult males in pinnipeds.
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29 **Material and methods**

30 **Study site**

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32 113 The study was conducted at Pelican Point Cape fur seal breeding colony (25°52.2'S,
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34 114 14°26.6'E), Walvis Bay, Namibia from 12th December 2019 to 6th February 2020, during the
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37 115 breeding season. Pelican Point is a sandy peninsula with homogenous and flat topography,
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39 116 roughly 1 km wide and 10 km north to south with most seals (and all field work) clustered in
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42 117 the northern ~3km. There is no recent published data on the number of individuals at Pelican
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44 118 Point but a 2011 survey reported 12.000 pups (Ministry of Fisheries and Marine Resources,
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46 119 unpubl. data) so there would be the same number of females as each female gives birth to a
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49 120 single pup each year. The ratio in harems averages 1 male to 30 females (harems size ranging
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52 121 from 7 to 66 females) (Riedman 1990; Nowak and Walker 2003), so the number of adult
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54 122 territorial males (> 8-13 years old) is estimated to be around 400 on the peninsula, with likely
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57 123 3 to 4 times as many subadult males (~3-8 years old). Throughout the breeding season, harems
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125 are distributed all around the point, close to the shore, mostly on the protected waters of the
126 eastern side (MM pers obs). Some groups of non-breeding juveniles (one- or two-year old
127 individuals) and subadult males (sexually but not socially mature) are observed on the vicinity
128 of the breeding colony.

129

130 This study is composed of two main components – describing the acoustic features of barks and
131 sequences of barks from territorial adult males within the colony under three different levels of
132 arousal. Secondly, we used playback experiments to investigate the behavioural responses of
133 subadult males to the series of adult male barks.

134

135 **Recording and describing the territorial adult males' barks in different behavioural** 136 **contexts**

137 *Recording procedure* - Recordings were made of focal adult bulls identified through
138 paint marking applied for associated research questions (oil-based paint marks applied to
139 individuals using a roller and pole, Martin et al. *in revision a*), natural scarring, or spatial
140 distribution within the colony (GPS location). To avoid resampling the same unmarked
141 territorial males, recordings were performed at different locations within the colony. Adult
142 males' barks were recorded using a Sennheiser ME67 directional shotgun microphone
143 (frequency range: 40 - 20000 Hz, sensitivity: 50mV/Pa \pm 2.5 dB) using a 44.1 kHz sampling
144 rate and connected to a two-channel NAGRA LB digital audio recorder. The distance between
145 the calling animal and the microphone ranged from 3 to 6 meters (visual estimation). While
146 recording, the experimenter described the social context and the behaviour of the barking
147 individual in a lapel microphone connected to the second channel. For this study, we only used
148 behaviours and activities of territorial males during barking. Behaviours were categorized into
149 three main contexts corresponding to different arousal states: (1) 'Standard activity' referred to

150 activities with a low arousal state and included non-directed (or spontaneous) barks produced
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2 151 to advertise his presence, and those made during interactions with females within his harem
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4 152 (i.e., herding, nuzzling), excluding mating. (2) ‘Confrontation’ corresponded to a high arousal
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7 153 state and involved the focal male reacting to another male approaching or entering his territory.
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10 154 Barks were directed towards the intruder and were associated with both non-physical (chasing)
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12 155 and physical interactions (fight) between the two individuals. (3) ‘Mating’ referred to barks
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14 156 produced during a copulation event, which may act to advertise dominance/success towards
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17 157 other males, or be directed towards the focal female.

18
19 158 *Acoustic analysis* - Recordings were resampled at 22.05 kHz as none of the barks’
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22 159 frequencies exceeded 10 kHz (Martin et al. *in revision*). The acoustic analysis of barks was
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24 160 performed using Avisoft SAS Lab Pro (R. Specht, version 5.2.14, Avisoft Bioacoustics, Berlin,
25
26 161 Germany) and barks were visually inspected on spectrograms calculated with a 1024-point fast
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28
29 162 Fourier transform (FFT), 75% overlap and a Hamming window. Five good-quality barks (i.e.
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31 163 with low background noise and no overlap with other vocalizations) were selected per sequence
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34 164 and a minimum of 3 different sequences (5 barks per sequence) were analysed per behavioural
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36 165 context for each individual (so at least 15 barks per individual per context were measured).
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39 166 Selected sequences were individually high-pass filtered at 100 Hz because most of the
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41 167 background wind noise was between 0 and 100 Hz. A set of nine acoustic features were
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44 168 measured for each bark: total duration of the call (*Dur*; ms), fundamental frequency (*f0*; Hz),
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46 169 frequency value of the 1st, 2nd and 3rd energy peaks (*Fmax1*, *Fmax2*, *Fmax3*; Hz), quartiles of
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49 170 energy spectrum (*Q25*, *Q50*, *Q75*; Hz) and the proportion of energy below 500 Hz (*Ebelow500*;
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51 171 %) from the averaged energy spectrum (Hamming window, frequency range for analysis: 0-
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53 172 5000 Hz). A 10th feature, the production rate of barks (*Barkrate*; Hz) was measured for three to
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56 173 five sequences within each behavioural context for each adult male.

174 *Statistical analysis* – Pairwise comparisons of the ten measured acoustic variables
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2 175 between the different behavioural contexts were carried out using a Wilcoxon Signed Rank test
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5 176 for paired samples in R (R Development Core Team 2020).
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10 178 **Playbacks: Behavioural responses of subadult males to the playback of adult barks**

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12 179 We tested the subadult male's response to barks produced at different rates through
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14 180 playback experiments. Playback experiments were performed over the course of 17 days with
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17 181 one to three experiments per day. Trials consisted of observing the behavioural response of
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19 182 resting subadult males to the broadcast of barks recorded from a territorial adult male (i.e. the
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22 183 stimulus).
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26 185 *Creation of stimuli* - We built eight playback tracks with bark sequences from eight
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29 186 different territorial males. Each playback track consisted of three bouts of barking (average
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31 187 duration 4.1 sec \pm SD 0.7 sec), recorded from the same territorial male and spliced together with
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34 188 a separation of 3 seconds between bouts. Note that no manipulation was made to the natural
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36 189 rate of each bark bout. We only used recordings made from individuals barking during standard
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39 190 activities to avoid any confounding effect of arousal state which may reflect in voice features.
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41 191 The bouts of barks used as stimuli were selected from all available bark bouts to have as wide
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44 192 a range of bark rates between individuals (i.e. between stimuli) as possible.
45

46 193 For analysis, a set of eight acoustic features were used to investigate the potential drivers
47
48 194 of the behavioural response of subadult males. *Barkrate* was calculated as a single average of
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50
51 195 the bark rates for all three bark sequences of a playback track. Seven spectral features (f_0 ,
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53 196 F_{max1} , Q_{25} , Q_{50} , Q_{75} , $E_{below500}$ and B_{dw12} , described in section 1) were calculated on each
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56 197 of the three bouts of the playback track. The three values obtained for each spectral feature were
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58 198 averaged to obtain a single value, later used in the statistical analysis.
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199 Providing high quality recordings is challenging in a very noisy CFS colony. Due to
200 limited high-quality recordings some playback stimuli had to be used more than once. To limit
201 pseudo-replication a total of eight stimuli tracks from eight different adult males were used and
202 the choice of a playback track was randomized for each experiment.

203

204 *Playback procedure* - In this study, subadult males were not individually identifiable
205 (marked) but given that they were both numerous and highly mobile (in contrast to territorial
206 males), and there were 1-13 days between trials, we are confident that the seals tested were
207 different on each day of the experiment and would consider the broadcasted barks as from
208 unfamiliar. Playbacks were performed on non-interacting subadult males that were resting,
209 either laying down or standing still. A single observer approached closely by crawling slowly
210 into the colony. When a suitable focal animal was identified the loudspeaker was manually
211 placed at 3 to 5 meters from the animal and not directly in his field of vision i.e. on his side to
212 facilitate the evaluation of his reaction. The observer moved back to 6 to 10 metres from the
213 focal animal and remained lying on the ground to minimise any disturbance. Once the observer
214 and equipment were settled, the behaviour of the target individual was monitored for two
215 minutes to ensure the subadult male was not actively engaged in an interaction with any other
216 animals, and was not obviously responding to the presence of the observer and so his
217 behavioural response could only be due to our playback stimulus. If no interaction was observed
218 during the 2-min observation period, we would broadcast the playback track. Stimuli were
219 broadcast using a waterproof and wireless high-powered speaker (JBL Charge 3, 2 x 10W,
220 frequency response: 65 HZ- 20 kHz) connected to a Bluetooth sound player (Sony NW-A35).
221 The amplitude level of the playback tracks was adjusted to the natural amplitude of male barks
222 at the range of 3 to 5 m (84 ± 2 dB SPL at 1 m, measured with a 'Testo 815' sound level meter,
223 A-weighting, fast-response).

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Behavioural analysis - Since there are many seals in the colony and interactions among individuals frequently occur, tested individuals were constantly exposed to external stimuli from neighbouring animals. To minimise these complications, the behavioural response of the target individual was only observed for 20 seconds from the start of the playback. If the tested individual was distracted/disturbed by another individual during the playback period, the experiment was excluded from the analysis. Response variables recorded were: latency (all latency measures in seconds) to look towards the speaker, look duration towards the speaker, latency to move (posture change or movement), distance of movement (away or towards the speaker, estimated by eye), latency to bark and the number of barks if produced. An absence of response was assigned a default value of 20s for latencies. The distance to move was relative and estimated as a ratio of the initial distance between the speaker and the focal animal. Values were positive for an approach towards the speaker and negative for a retreat (e.g. 0: no movement, 1: walked all the way to the speaker, -0.5: half way retreat). If the tested individual had been distracted/disturbed by another individual during the playback period, the experiment was excluded from the analysis. Since few subadult males reacted by producing barks, variables related to calling were not included in the analysis. We performed a principal component analysis (PCA) on the four behavioural variables: latency to look, look duration, latency to move and distance moved, to obtain a score of the behavioural response (McGregor 1992). The PC scores of the principal components (PC) with eigenvalues greater than 1 were used to quantify the level of response of subadult males to playbacks.

We investigated the relationships between the behavioural response of subadult males (i.e. PC scores) and the eight acoustic features measured from the played back bark sequences of adult males. As an initial test, the acoustic variables from adult males (*Barkrate* and the set

249 of 7 spectral features) were tested for multicollinearity at the level of 0.8. The variables *Q25*
250 and *Q50* were excluded because of their high correlation with other variables. All other
251 variables included in the analyse were normalized to account for differences in units of
252 measurement and ranges of values. Using a multiple linear regression in R (*lm* function, *base*
253 package, R Development Core Team 2020), we investigated the relationship between PC scores
254 and the final set of acoustic parameters (6 variables: *Barkrate*, *f0*, *Fmax1*, *Q75*, *Ebelow500* and
255 *Bdw12*). The normality and homoscedasticity of the residuals were visually verified.

257 **Results**

258 **Acoustic features of territorial adult males' barks in various behavioural contexts**

259 We recorded the barks from 47 territorial males for which, 14 were recorded in at least
260 2 different behavioural contexts (standard activity, confrontation or mating). As only four adult
261 males were recorded during copulation, statistical comparisons were not possible for this
262 context. The pairwise comparison of the 10 measured acoustic features revealed that, in spite
263 of our relatively small sample size ($n=10$), both the variables *Barkrate* and *f0* were significantly
264 lower during standard activity than during confrontation (Wilcoxon Signed Rank tests, $n = 10$,
265 $V = 55$, $p = 0.0059$ - same in both cases) (Fig. 1, Fig. 2). The bark rate increased by 17 % (0.55
266 Hz) on average between standard activity and confrontation, while the *f0* value increased by 20
267 % (22 Hz) on average. Other variables such as bark duration and spectral features did not show
268 any significant differences between these two behavioural contexts. Although not statistically
269 tested barks produced by a territorial male during mating were always produced at a faster rate
270 compared to the same individual barking in standard activity (Fig. 1a). However, no general
271 trend for the fundamental frequency value as well as for other features was found (on Fig. 1b.)

272 **Behavioural responses of subadult males to playbacks of territorial adults**

274 A total of 22 playback experiments on different subadult males were included in our
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2 275 analysis. Of these, 20 looked towards the speaker soon after they heard the playback (mean
3
4 276 latency to look: 3 ± 2.6 sec), and for a relatively long period of time (mean duration to look: 8.2
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7 277 ± 5.2 sec). A third of tested individuals (7/22) stood up and moved in response to the playback
8
9 278 with four moving towards and three males away from the speaker. Only three subadult males
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11 279 called back to our playback track, and one did not react at all.
12
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14 280 The behavioural responses were combined into a PCA and out of the four principal
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16 281 components generated, only the first PC (PC1) had an eigenvalue greater than 1. PC1 explained
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18 282 48.33 % of the total variance (Table 1) and was strongly correlated with the two response
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20 283 variables involving looking towards the loudspeaker: latency to look (negative correlation) and
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22 284 look duration (positive correlation) (Table 1). Positive values of PC1 scores corresponded to
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24 285 short latency to look (i.e. quick response) and a long period of looking, describing a vigilant
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26 286 behaviour. The two response variables involving movement of the subadult males i.e. latency
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28 287 to move and distance moved, were correlated with PC2 (Table 1) and were therefore excluded
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30 288 from the following analysis.
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36 289 The subadult males' responses (indicated by PC1 scores values) were investigated as a
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38 290 function of the acoustic parameters of the barks of the territorial adult male played back during
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40 291 the experiment using a multiple linear regression. Although only *Barkrate* and f_0 showed
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42 292 differences among the behavioural contexts, all acoustic variables were inspected because the
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44 293 duration or spectral features of a call can provide clues to the physical condition of the emitter,
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46 294 especially the body size (source-filter theory, Fant 1960; Taylor and Reby 2010) and can
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48 295 therefore influence the behavioural response of subadult males. Of all the acoustic parameters
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50 296 included in the model, *Barkrate* was the only variable with significant regression coefficients
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52 297 (Table 2): a positive relationship was found between PC1 scores and the playback bark rate.
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54 298 The multiple regression was therefore simplified to a simple regression between PC1 scores
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299 and *Barkrate* and presented in Fig. 3. As PC1 was highly correlated with the latency to look
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2 300 and the look duration, it means that as the *Barkrate* of the playback stimulus increased, the
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4 301 tested subadult males looked at the loudspeaker more quickly (i.e., lower latencies) and for a
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7 302 longer period of time. No significant relationships were found for other acoustic parameters (f_0
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10 303 and spectral features of barks, Table 2).

305 Discussion

306 Graded vocalisations allow animals to communicate different levels of information, emotional
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19 307 state or urgency by modifying only a few parameters of their vocal production. For instance,
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21
22 308 the rate, loudness and harshness of alarm calls vary with the type of predators or their spatial
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24 309 proximity in several species (Leger et al. 1980; Manser 2001; Leavesley and Magrath 2005).
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26
27 310 The bark is the primary call type used by male Cape fur seals (Martin et al. *in revision*). It serves
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29 311 in all social interactions corresponding to different arousal states: ‘patrolling’ their harem and
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32 312 advertising their presence, randomly interacting with females, insistently interacting with a
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34 313 particular female for the purpose of mating, copulating or chasing other males. In some other
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37 314 fur seal species, males use multiple types of vocalizations (e.g. threat calls, growls or
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39 315 submissive calls, Pierson 1987; Phillips and Stirling 2001; Page et al. 2002; Tripovich et al.
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41 316 2008a) enabling them to modulate their vocal production with context and allow receivers to
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44 317 more clearly interpret their behavioural intentions (Phillips and Stirling 2001) (Phillips and
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46 318 Stirling 2001). For instance, in South American fur seal, the use of a full threat call is a signal
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49 319 of high arousal state and a willingness to fight, while submissive calls rather show an attempt
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51 320 to retreat (Phillips and Stirling 2001). For this reason, within the constraints of the restricted
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54 321 vocal repertoire Cape fur seal males, coding arousal state in barks rates would be an advantage.

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56 322 In colonial species, call redundancy (i.e. repetition of an identical signal) is a widely
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58 323 used strategy allowing individuals to increase the probability of being heard in such noisy
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324 environments (Mathematical theory of information, Shannon and Weaver 1949). For example,
325 colonial seabirds such as penguins use redundancy in their calls (Lengagne et al. 1999; Aubin
326 and Jouventin 2002; Gemard 2020), and Otariids commonly produce sequences of barks
327 (Peterson et al. 1968; Stirling and Warneke 1971; Roux 1986; Fernández-Juricic et al. 1999;
328 Phillips and Stirling 2001; Page et al. 2002; Tripovich et al. 2008a). Previous studies have
329 shown the high information potential of barks: with barks reported to convey information
330 relative to species recognition (Gwilliam et al. 2008), individual identity (Fernández-Juricic et
331 al. 1999; Tripovich et al. 2005; Gwilliam et al. 2008), neighbour-stranger recognition (Roux
332 and Jouventin 1987; Tripovich et al. 2008c; Attard et al. 2010) and even geographical variation
333 (Attard et al. 2010; Ahonen et al. 2014; Martin et al. 2021, *in revision*). To our knowledge,
334 investigations of the emotional and motivational state encoded in pinnipeds' vocalizations have
335 so far mainly focused on mother and pup calls (e.g. Perry and Renouf 1988; Charrier et al. 2002;
336 Collins et al. 2011) and little is known about the territorial or agonistic calls of males and the
337 emotional information encoded in bark rates (Fernández-Juricic et al. 2001; Charrier et al.
338 2011).

339 In the first part of this study, we reported significant changes in some acoustic features
340 and the production rate of barks depending on the context of production and the level of
341 motivation of Cape fur seal males. In line with our predictions and former assumptions among
342 Otariids, our dataset revealed an increase of the bark rate produced by males during high-
343 arousal events (i.e. confrontation) compared to standard activities (i.e. spontaneous barks). Such
344 an increase of the bark rate is consistent with studies on birds and mammals which have shown
345 that the call rate is a powerful way of coding emotions and motivation states (Rendall 2003;
346 Yin and McCowan 2004; Geberzahn and Aubin 2014; Gemard 2020). Repeated vocalisations
347 enhance signal detectability (Schleidt 1973). Moreover, an increase of the signal-to-silence ratio
348 makes the call sequence sound louder thus exhibiting a higher degree of hostility (Yin and

349 McCowan 2004). Faster barks may thus appear easier to detect in the noisy environment of the
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2 350 colony, but could also evoke the presence of a threatening opponent.
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5 351 In addition, variations in the bark rate were accompanied by an increase in the
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7 352 fundamental frequency (f_0) during high arousal state contexts. Variations in motivational or
8
9 353 emotional state were claimed to lead to changes in the fundamental frequency of mammalian
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11 354 vocalisations such as in sheep (Sèbe et al. 2012), baboons (Rendall 2003), common marmosets
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13 355 (Yamaguchi et al. 2010), bats (Bastian and Schmidt 2008), or Weddell seals (Collins et al. 2011)
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15 356 among many others (for full review see Briefer 2012). The fundamental frequency
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17 357 characterized the first step of the two-stage process of vocal production known as the ‘source-
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19 358 filter theory’ (Fant 1960; Taylor and Reby 2010). It refers to the rate of opening and closing of
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21 359 the glottis under the pressure of an air-flow from the lungs. Primarily driven by the length and
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23 360 mass of the vocal folds, f_0 is assumed to be a relatively constant parameter, but can vary due to
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25 361 modifications in muscular tension in the vocal folds, sub-glottal pressure or changes in airflow
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27 362 from the lungs (Taylor and Reby 2010). In our study case, shifts in f_0 between various contexts
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29 363 of production are likely to be linked to modifications in the male’s behaviour. In fact, during
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31 364 fighting and mating, males are involved in a more active muscular effort than during standard
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33 365 activity, and thus muscle tension might change their fundamental frequency. Therefore, these
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35 366 f_0 changes are likely produced in a less intentional way than Bark rate variations as f_0 variations
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37 367 are linked to the vocal tract anatomy. Indeed, if captive pinnipeds have been shown to be
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39 368 capable of some vocal motor control after training and reinforcement (Reichmuth and Casey
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41 369 2014; Stansbury and Janik 2019), under natural circumstances as studied here, such variations
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43 370 of the fundamental frequency are more likely resulting from changes in the somatic and
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45 371 autonomic nervous system induced by emotions, and thus non-intentionally produced and can
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47 372 be considered an honest signal of emotional state.
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373 In the second part of the study, we tested if subadult male seals can perceive these
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2 374 variations in bark series from different adult males and thus adapt their behaviour in accordance.
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5 375 In general, the broadcasting of a territorial male's barks led to a rapid increase in the vigilance
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7 376 of the target individuals which looked towards the sound source for an average of 3 seconds
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10 377 after the start of the experiment. This is intuitive as bulls tend to chase subadult males away
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12 378 from their harem, and therefore represent a real threat to subadult males that are smaller and
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14 379 less competitive than bulls in the case of a fight. As subadult males roam in the entire breeding
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16 380 colony, they are likely not familiar with individual territorial bulls, and thus assessing the threat
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19 381 level from their vocalisations is the only way to adjust their behaviour, and ensure survival.
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22 382 Here, we found that subadult males preferred to keep a low profile (i.e., remained lying down)
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24 383 rather than an active retreat. Similar results were found in male northern elephant seals when
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26 384 immature males were exposed to calls from mature males (Casey et al. 2020). In colonial
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28 385 environments where the densities of individuals are high, this strategy seems advantageous for
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30 386 both individuals: territorial males save energy by not fighting subadults as long as they do not
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32 387 compromise the integrity of their harem (i.e. by attempting to mate with females) and subadults
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34 388 avoid unnecessary escape impulses. The weak reaction of subadult males to these playback
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36 389 experiments also highlighted the importance for social species of using multi-modal signals in
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38 390 their interactions. In this case of dominance among males, the behavioural response of subadult
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40 391 males in response to vocalisations produced by an adult (resulting in increased vigilance) could
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42 392 be enhanced by a visual cue (i.e. the sight of a territorial bull approaching). Acoustic signals
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44 393 may therefore serve as an initial warning signal that would be corroborated (or not) by the
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46 394 occurrence of a visual cue. The simultaneous presence of multiple cues is known to modulate
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48 395 the receiver's response (Partan and Marler 1999) and thereby may benefit communication
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50 396 processes (Ay et al. 2007; Ratcliffe et al. 2016; Wierucka et al. 2018).
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397 Secondly, our experiments revealed that Cape fur seal subadult males' response to the
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2 398 broadcast of territorial males' barks could vary with the bark rate of the stimulus. This
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5 399 reinforces previous findings stating that pinnipeds have the sensory and cognitive abilities to
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7 400 decipher rhythm in acoustic signals and are able to process them in order to modulate their
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10 401 social behaviour (Cook et al. 2013; Mathevon et al. 2017) Similar results were found in
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12 402 Australian sea lions in which bark rate was used by males to estimate the potential threat from
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14 403 a rival (Charrier et al. 2011). No other acoustic parameters such as the fundamental frequency
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17 404 value (f_0) or spectral features seemed to influence the behavioural response of subadults. Since
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19 405 these are individualized parameters and containing information about the anatomy of the calling
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22 406 territorial male (e.g. body size; Taylor and Reby 2010), this indicates that subadult males did
23
24 407 not specifically react to the phenotype-linked acoustic cues of territorial males but to their bark
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27 408 rate indicating their arousal state. It contrasts with previous studies on mammals responding
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29 409 more to vocalizations with changes in 'source-related' acoustic features (Charlton et al. 2010;
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32 410 Taylor et al. 2010).

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34 411 We previously showed that the bark rate of a territorial male varied with behavioural context
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36 412 and arousal state. In these playback experiments, all broadcast barks were recorded in the same
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39 413 context (i.e. standard activities) to avoid confounding effects. Subadult males responded with a
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41 414 significantly higher level of vigilance to broadcast sequences with faster bark rates. This
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44 415 revealed that even for barks produced during low arousal standard activities, bark rate is
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46 416 regarded as a threat level indicator. Because the fundamental frequency value is often filtered
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49 417 by the vocal tract of the emitter and therefore difficult to perceive, the bark rate seems the
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51 418 unique way to assess the arousal state of a territorial male for subadults. Further experiments
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53 419 where subadult males will be tested with barks recorded in different contexts of production
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56 420 should reveal even stronger results.

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421 This study is the first investigation in pinnipeds coupling the coding of the arousal-state in
422 territorial males' vocalisations and the decoding processes by subadult males. This knowledge
423 allows us to better understand the communication network of social species and the
424 involvement of acoustic signals in their interactions. Further investigations on different
425 behavioural contexts such as male-female interactions or mating would be interesting to carry
426 out to understand whether females could use males' vocalisations to identify their harem holder
427 and facilitate orientation within the colony when they return from foraging at sea.

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Tables

Table 1 Summary of the principal component analysis (PCA) performed with four behavioural responses variables. *Bold values show behavioural variables highly correlated to the first two principal components*

	PC1	PC2	PC3	PC4
Eigenvalues	1.93	0.99	0.74	0.28
% cumulative variance	48.33	73.08	92.94	100
Correlation coefficients between PC and variables				
Latency to look	-0.79	0.50	0.03	0.34
Look duration	0.89	-0.22	0.09	0.39
Latency to move	-0.51	-0.54	0.68	0.03
Displacement distance	-0.50	0.64	0.57	-0.12

Table 2 Multiple linear regression analysis of barks' acoustic parameters broadcast during the playback on subadult males' behavioural response (PC scores)

	PC1 scores		
	β	SE	<i>p</i>
<i>Barkrate</i>	1.024	0.303	0.0041*
<i>f0</i>	0.011	0.482	0.982
<i>Fmax1</i>	-0.396	0.479	0.421
<i>Q75</i>	-0.166	0.441	0.712
<i>Ebelow500</i>	-0.396	0.391	0.327
<i>Bdw12</i>	0.834	0.489	0.109

Figure captions

1
2 **Fig. 1** Median values with first and third quartiles (lower and upper hinges) and interval
3 between the smallest and the largest values (whiskers, no further than 1.5*IQR from the hinge)
4 of adult males' *Barkrate* (**a**) and *f0* (**b**) in the three contexts of bark production. *Grey lines*
5 *represent the difference in the median values of Barkrate and f0 for the same adult male between*
6 *two different contexts of production*
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12 **Fig. 2** Spectrograms of a sequence of barks produced by the same territorial male in standard
13 activity and during a confrontation with another male (**a**) and the overlaid energy spectrum of
14 one example bark from each context (**b**)
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19 **Fig. 3** Behavioural response of subadult males indicated by PC1 scores to playbacks with
20 different *Barkrate* values (in Hz). *Linear regression: $F(1,20) = 6.631$, $p = 0.018$, adjusted R^2*
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Figure 1

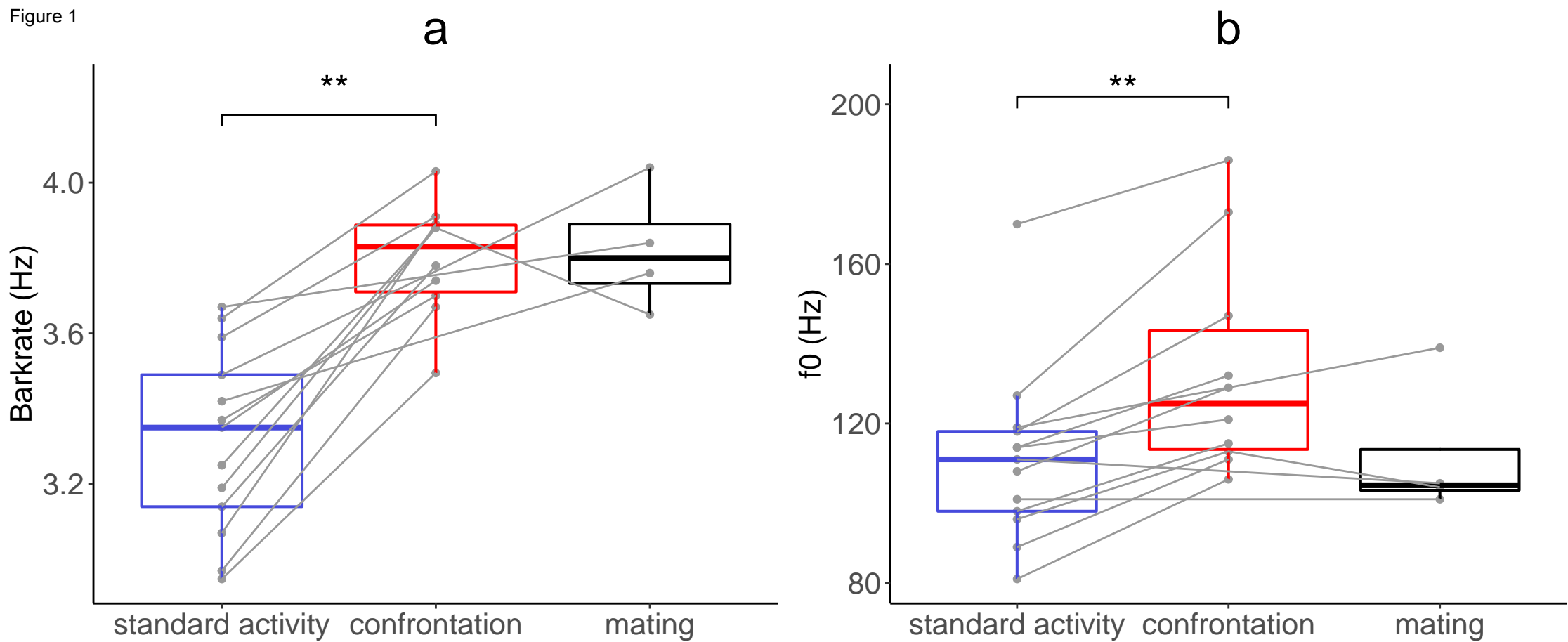


Figure 2

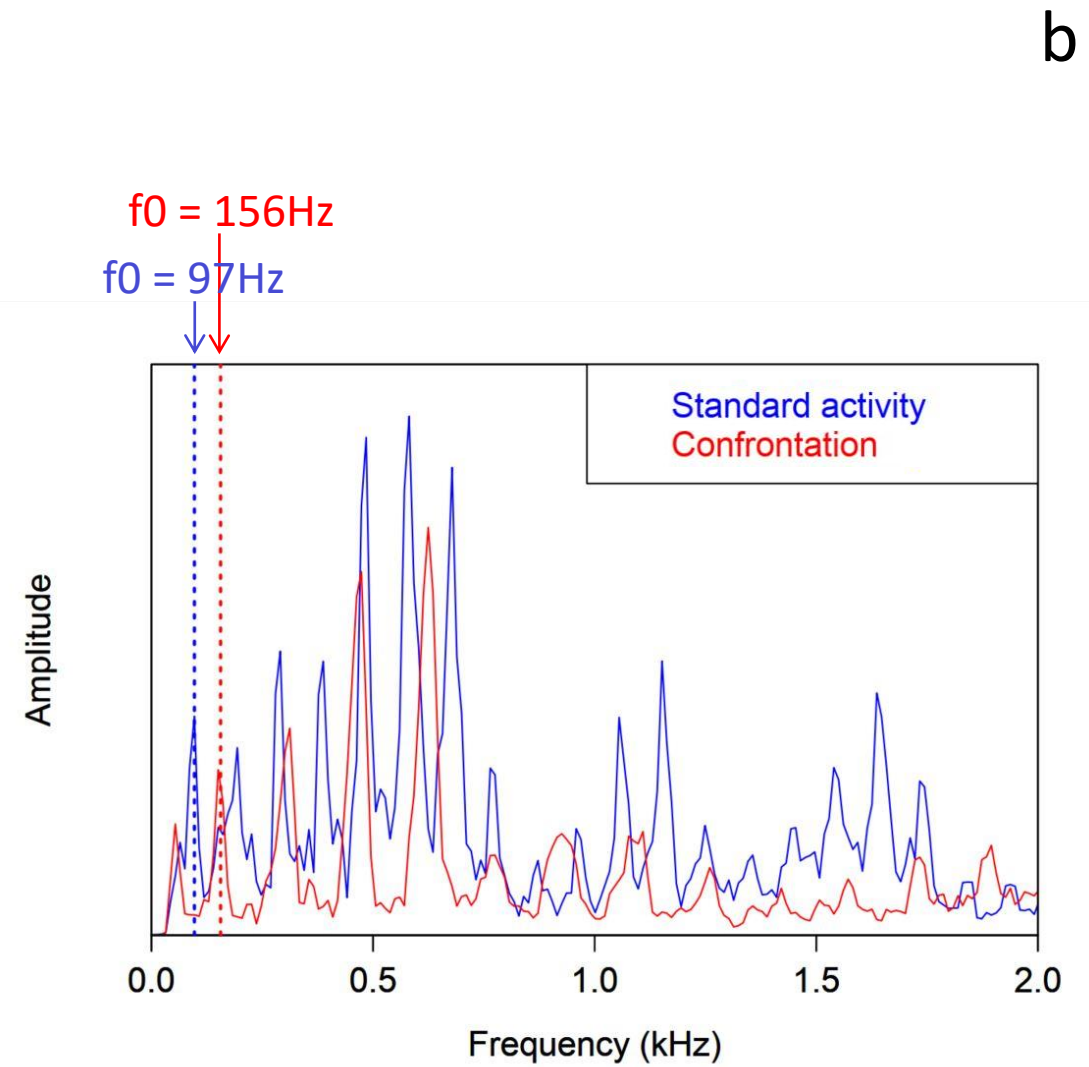
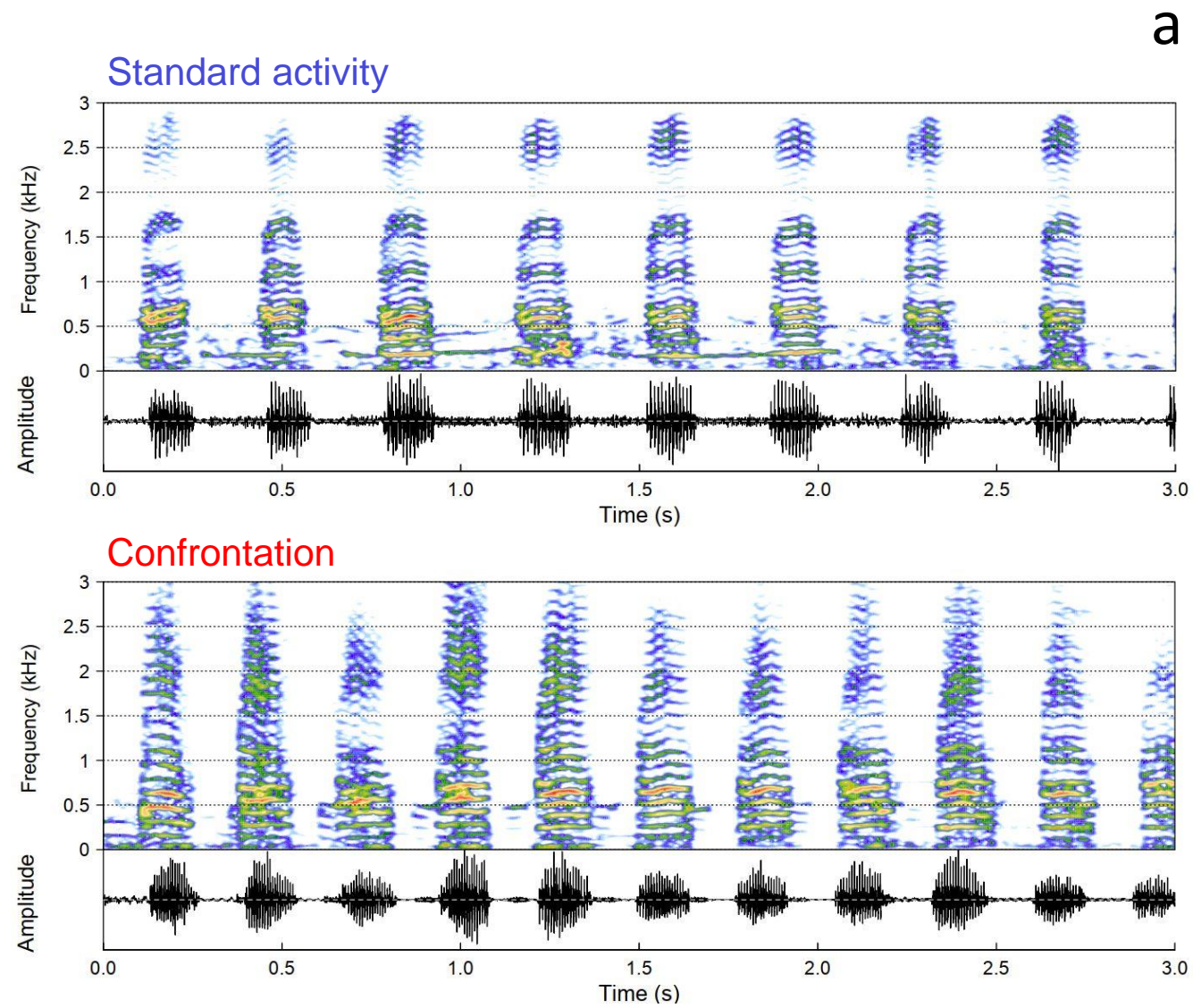


Figure 3

