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Mutual mother-pup vocal recognition in the highly colonial Cape fur seal: evidence of discrimination of calls with a high acoustic similarity

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Abstract

1
2 The Cape fur seal (*Arctocephalus pusillus pusillus*) is one of the most colonial mammal species in the
3 world. Females exclusively nurse their pups for 9 to 11 months, during which they alternate frequent
4 foraging trips at sea with suckling periods ashore. The survival of the pup thus depends on the ability of
5 the mother-pup pair to relocate each other among thousands of individuals. Previous work has
6 demonstrated identity information encoded in pup-attraction (PAC) and female-attraction (FAC) calls.
7 Here, we investigated vocal recognition between mother and pup using playbacks of PAC and FAC
8 performed during the breeding season at Pelican Point, Namibia. Both females and pups were able to
9 specifically discriminate the voice of their pup or their mother from non-affiliated pup or mother.
10 Females were able to memorize previous versions of their pup's calls (evidence of recognition up to 73
11 days after pup's calls recording). Vocal recognition was demonstrated in pups from 1- to 13-weeks old
12 age. Females and pups did not respond differently to the non-filial or non-mother (for pups) stimulus
13 even if it had a strong acoustic similarity with the filial or mother stimulus. This suggested that Cape fur
14 seal mother-pup pairs have high perceptual and cognitive abilities, allowing individuals to identify kin's
15 vocalizations in a very noisy and confusing environment.

Keywords

16
17
18 Vocal communication – Individual recognition – Mother-young interaction – Acoustic similarity –
19 Ecological constraints – Cape fur seal

Introduction

20

21 Parental care is a key component of reproduction in many animal species (Clutton-Brock 1991).
22 It includes all parental behaviours presumed to increase the offspring's chance of survival and can thus
23 take many forms (e.g. nest building, guarding and feeding of young). Although these behaviours are
24 advantageous to the adults as they enhance their reproductive success, parental investment is always
25 associated with a significance expense of time and energy (Trivers 1974). The costs related to rearing
26 young are linked to the reproductive strategies of the species. Factors that can influence the level of
27 energy expenditure are the brood size, the duration of the neonatal dependency period and whether
28 parental care is provided by a single parent or both (Winkler 1987). A significant way to optimise
29 parental investment and reduce costs by avoiding misdirected care is the establishment of parent-
30 offspring recognition (Halliday 1983). Multiple sensory modalities (i.e. vocal, visual, olfactory and
31 spatial) can be involved in individual recognition. However, in birds and mammals this relies heavily
32 on vocal signals (i.e. vocalizations) (Aubin and Jouventin 2002; Beecher et al. 1981; Charrier et al.
33 2001b; Knörnschild and Von Helversen 2008; Müller and Manser 2008; Sèbe et al. 2010; Trillmich
34 1981).

35 The use of vocal cues for mother-young recognition has been widely investigated in the highly
36 vocal clade of pinnipeds (i.e. true seals, fur seals, sea lions and walruses) (for review see Charrier 2020).
37 Among pinnipeds, species face different levels of selective pressures for mother-young recognition
38 depending on their social structure and reproductive strategies. Indeed, their animal density (solitary or
39 colonial), breeding system (monogamous or polygynous), and maternal attendance (the duration of the
40 lactation period, level of allonursing) vary greatly among species. In general, Otariids (i.e. fur seals and
41 sea lions) show the highest level of ecological constraints (or selective pressures) which may shape the
42 characteristics of mum-pup recognition in densely populated colonies. Females exclusively nurse their
43 young for a long time (from 4 months to 2-3 years) while alternating foraging trips at sea with ashore
44 suckling period (Riedman 1990). In comparison, phocid species (i.e. true seals), with the exception of
45 highly colonial species such as elephant and grey seals, are under lower selective pressures for
46 recognition as they live either solitary or in small groups. Moreover, most female phocids stay in close

47 proximity to their young whom they nurse for a shorter time (from few days to several weeks) (Riedman
48 1990). Investigation of individual vocal signatures as well as experimental studies using playback in
49 multiple pinniped species have revealed marked differences in the complexity level of their recognition
50 systems according to the degree of selective pressures they face (Charrier 2020). Mutual mother-pup
51 vocal recognition has been demonstrated in most Otariid species investigated, with a rapid onset within
52 a few days of birth (before the first mother's foraging trip at sea) and a high level of individuality in their
53 calls (Charrier et al. 2001a, 2002b, 2009; Fernández-Juricic et al. 1999; Insley 2001; Page et al. 2002;
54 Pitcher et al. 2009, 2010, 2012; Trillmich 1981; Tripovich et al. 2006, 2009). In contrast, species with
55 lower selective pressures such as non-colonial phocids seemed to exhibit uni-lateral vocal recognition,
56 a moderate to low degree of individuality in their vocalizations and a delayed onset of recognition
57 (Collins et al. 2005, 2006; Insley 1992; Job et al. 1995; McCulloch and Boness 2000; McCulloch et al.
58 1999; Sauvé et al. 2015; Van Opzeeland et al. 2012).

59 The Cape fur seal (*Arctocephalus pusillus pusillus*) is the pinniped species with the greatest
60 ecological constraints on individual vocal recognition due to their extreme colonial life. Indeed, Cape
61 fur seal (CFS) are the most colonial pinniped species (and one of the most colonial mammals in the
62 world), with colonies of several hundreds of thousands of individuals formed during the breeding season
63 (210,000 individuals annually at Cape Cross seal reserve in Namibia; Ministry of Environment and
64 Tourism, 2021). Females give birth to a single pup each year between mid-October and early January
65 (De Villiers and Roux 1992; Rand 1967). Throughout lactation period, which lasts 9 to 11 months
66 (David and Rand 1986), maternal attendance periods on shore are interspersed with foraging trips at sea
67 throughout. Following parturition, Cape fur seal mothers undertake their first foraging trip at sea earlier
68 than other otariid species – on average 6 days after giving birth (David and Rand 1986). The mean
69 duration of the first postpartum absence is 2.3 days and the duration of foraging trips by mothers
70 increases progressively in the first 90 days of the pups' life (David and Rand 1986). Overall, females
71 are absent for approximately 70% of the time until weaning (Gamel et al. 2005). In addition, fostering
72 or allo-suckling is uncommon in this species (Rand 1955; Riedman 1990) and as in other otariid species,
73 females can be highly aggressive toward non-filial pups (Harcourt 1992).

74 Like other fur seal species, Cape fur seal females and pups use in-air vocalizations to
75 communicate with each other. These acoustic signals are exchanged at both long distances, i.e. in the
76 context of reunion when the female returns from a foraging-trip, and at short range, close contact i.e.
77 when mother and pup are reunited in the colony (Martin et al. 2021a). Individual stereotypy in contact
78 calls produced by CFS mothers and pups is high and supported by the duration, the fundamental
79 frequency and the energy spectrum (Martin et al. 2021b). These calls therefore allow a reliable
80 individual identification in the colony. However, the existence of an individual vocal stereotypy does
81 not prove that individuals effectively use these signals to identify each other. Despite extensive studies
82 on mother-pup vocal recognition in pinnipeds, the vocal recognition in CFS has yet to be demonstrated.

83 The first objective of the present study was to assess the occurrence of mother-pup vocal
84 recognition in this species through a series of acoustic playback experiments. Based on the extensive
85 literature of vocal recognition in pinnipeds and behavioural observations, we hypothesized that acoustic
86 signals produced by females and pups are effectively involved in the mother-pup reunion process and
87 that the recognition would be mutual: mothers and pups would be able to specifically recognize each
88 other's calls.

89 Mother-pup vocal recognition is based on learning and memorising the voice i.e. the acoustic
90 parameters specific to a related individual (mother or pup). We have previously demonstrated significant
91 ontogenetic changes in the CFS pups' voice over the first months of life (Martin et al. 2021a) whereby
92 pups produce calls of longer duration, with energy more evenly distributed among the harmonics and
93 with a lower proportion of bleating (i.e. fast frequency modulation) (Martin et al. 2021a). Changes in
94 these acoustic parameters which are known to support individual vocal stereotypy (Martin et al. 2021b)
95 may complicate vocal recognition of filial pups. Indeed, in order to maintain recognition, females may
96 have to learn new versions of their pup's call over time. Long-term vocal recognition has been
97 demonstrated in several species, even when there are substantial changes in pups' calls. For example,
98 female Subantarctic fur seals (*Arctocephalus tropicalis*) still recognized their pup's voice after several
99 months (Charrier et al. 2003a). The second objective of the present study was to investigate

100 modifications in the recognition of a pup's calls by its mother by examining how Cape fur seal females
101 responded to playback of their own pup recorded several weeks earlier.

102 The third part of our study aimed to evaluate the efficiency of the individual vocal recognition
103 in a colonial environment. As mentioned earlier, the selective pressures for mother-pup individual
104 recognition are high in group-living species since it is crucial for pups' survival and females'
105 reproductive success. However, in very dense colonies as found in Cape fur seals, thousands of
106 individuals interact and vocalize at the same time resulting in a very noisy and confusing environment.
107 The extreme gregariousness of this species greatly compromises the discrimination of acoustic signals.
108 Despite an important degree of individual stereotypy in their vocalizations (Martin et al. 2021b), calls
109 produced by females (and calls produced by pups) all have the same general structure and show
110 overlapping acoustic characteristics among individuals (temporal and spectral, Martin et al. 2021b). In
111 addition, the possibilities of coding individual signatures are relatively limited due to a small number of
112 individualised acoustic parameters (Martin et al. 2021b). Discriminating individuals by their voice thus
113 requires fine auditory perception abilities allowing both females and pups to detect subtle inter-
114 individual variations in their calls. Here, we investigated how females and pups responded to two stimuli
115 with different degrees of acoustic similarity to evaluate their perception abilities and their influence on
116 their behavioural responses. We hypothesized that two stimuli with high similarity could induce a less
117 discriminative behavioural response, whereas an animal exposed to two very distinct calls should show
118 strongly contrasted responses.

119 **Methods**

120 **Study site and animals**

121 The study took place at the Pelican Point Cape fur seal breeding colony, Namibia (25°52.2'S,
122 14°26.6'E). The experiment was conducted from mid-November 2019 to mid-February 2020, during
123 and after the breeding season. In order to recognize mother-pup pairs for recordings and playback trials,
124 pups were bleach-marked using hair-dye (Blonde high-light kit, ©Kair) at the beginning of the pupping
125 season. The marks consisted of numbers applied on their flank using a 10-cm wide wooden pad attached

126 to the end of a 5-metre pole. Although the marking procedure is minimally invasive and performed at a
127 distance, we reduced disturbance by not marking the mothers. Females were identified through their
128 association with their marked pup. As allonursing is very rare in CFS (Riedman 1990), a female nursing
129 a pup was considered as her filial pup. Whenever possible, we used the visual aspect of the pups'
130 umbilical cord to estimate their age (Martin et al. 2021a). Very small pups that had a fresh and/or long
131 umbilical cord were considered to be less than one week old. The slightly larger pups with very short
132 and dry cord remains were categorised as less than 2 weeks old. Pups that already had no umbilical cord
133 on the day of dye-marking were classified as unknown age.

134 **Recording procedure**

135 Mothers and pups were recorded when calling to each other - respectively producing pup
136 attraction calls (PAC) and female attraction calls (FAC). If a pup had just been marked, a 15-minute
137 waiting period was taken before recording it to allow the pup to return to a baseline behaviour.
138 Vocalisations were recorded using a Sennheiser ME67 directional shotgun microphone (frequency
139 range: 40 – 20.000 Hz +/- 2.5 dB) at 44.1 kHz sampling frequency connected to a two-channel NAGRA
140 LB or Roland R26 digital audio recorder. In order to assign the calls to the correct individual, the
141 experimenter gave the identity (i.e. the pup's mark number) of the animal vocalizing in a lapel
142 microphone connected to the second channel. Distance from focal animals ranged from 0.5 to 6 meters
143 during recording sessions.

144 **Playback procedure**

145 Playback stimuli were prepared using Avisoft SAS Lab Pro (R. Specht, version 5.2.14, Avisoft
146 Bioacoustics, Berlin, Germany) and GoldWave v.6.54 (GoldWave Inc, 2021). The number of calls and
147 the silence interval between calls is highly variable across individuals and behavioural or motivational
148 contexts. Series consisted of 6 calls from the same individual, each separated by 2 seconds of silence,
149 representing a natural calling rate within the species range. The tracks had an average duration of 16.50
150 ± 2.43 s for females' calls and 14.10 ± 1.55 s for pups' calls. Most of the tracks consisted of 6 different
151 calls. In some cases, individuals were not very vocal and we could not get 6 good-quality calls for the

152 playback series, thus we had to replicate some of the calls in the playback series. Calls were high-pass
153 filtered at 100 Hz to remove background noise. Since the average fundamental frequency of the calls is
154 higher than 100 Hz (264 ± 41 Hz for PAC and 364 ± 79 Hz for FAC; Martin et al. 2021a), such filtering
155 did not affect the spectrum of the broadcast vocalizations.

156 Females were tested in presence of their young, with the speaker on the opposite side of their
157 pup. Pups could be tested during the absence of their mother (i.e. the female was away from her pup or
158 foraging at sea). Each focal individual was exposed to two stimuli series within a trial: a series of calls
159 recorded from a related individual i.e. the focal pup's own mother or the focal female's own pup - and
160 a series of calls recorded from an unrelated individual. Non-filial pups' and non-mothers' vocalizations
161 were chosen at random from recordings made during the same breeding season and from the same
162 breeding colony. The two playback series were separated by at least 5 minutes and the order of the series
163 was randomized. Calls were broadcast using a waterproof and wireless high-powered speaker (JBL
164 Charge 3, 2 x 10W, frequency response: 65 Hz- 20 kHz) connected to a Bluetooth sound player (Sony
165 NW-A35). The amplitude level of the playback tracks was adjusted to the natural amplitude of PAC and
166 FAC (respectively 88 ± 2 dB SPL at 1 m and 80 ± 2 dB SPL at 1 m, received levels measured with a
167 'Testo 815' sound level meter). The speaker was placed from 1 to 3 meters from the focal individual at
168 45 to 90° orientation to induce searching behaviour and thus facilitate the evaluation of a behavioural
169 reaction. Playback experiments were filmed using a Fujifilm FinePix XP90 camera to allow further
170 analysis.

171 **Behavioural response**

172 Responses to the playback series were all assessed through video analysis with the software
173 BORIS (Friard and Gamba 2016). Since CFS breeding colonies are very dense and many individuals
174 vocalise simultaneously, the behavioural response of the focal individual (female or pup) was observed
175 for 20s (after the beginning of the playback) only to ensure that the reaction was related to played back
176 calls and not to an external stimulus (i.e., other vocalising individuals). Response variables were latency
177 to look towards the speaker (s), look duration towards the speaker (s), latency to move (posture change
178 or movement, s), latency to call (s) and number of calls. An absence of response was assigned a default

179 value of 20s for latencies. For females, we also noted whether they verified the presence of their pup by
180 their side (visual and/or olfactory check). However, if the focal individual was distracted or disturbed
181 by another individual during the playback session or did not respond at all to both stimuli (e.g. sleeping
182 or unmotivated animal), the trial was excluded from the analysis, and the individual was tested another
183 day.

184 **Statistical analysis**

185 The overall behavioural response of each focal individual was obtained by combining the raw
186 data of the 5 response variables in a principal component analysis (PCA). Principal components (PCs)
187 with eigenvalues greater than 1 were retained (Kaiser's criterion) and corresponding PC scores were
188 used as a composite score to quantify the level of response of tested individuals (McGregor 1992).

189 *Mother's behavioural response.*

190 First, a Wilcoxon paired signed rank test was used to compare PC scores of females between
191 filial and non-filial pups' calls (non-parametric test because of non-normal data). Then, the responses of
192 mothers to their own pup's vocalizations the (filial stimulus) were compared according to whether
193 females visually and/or olfactory checked for the presence of their pup using a Wilcoxon rank sum test.
194 Finally, we used a linear regression to investigate the mother's response to the filial stimulus according
195 to the time elapsed between the recording date of the pups call (the 6 female-attraction calls composing
196 the playback track) and the playback trial (in days) (significance level $\alpha = 0.05$).

197 *Pups' behavioural response.*

198 Similar to females, a Wilcoxon paired signed rank test was used to compare PC scores of pups
199 to mother's and non-mother's calls. Secondly, the responses of pups to the playback series were
200 investigated according to their age at the time of the experiment (in weeks). Two univariate linear
201 regressions were used to assess the relationships between pups' age and their response to the mother
202 playback (PC scores mother), and between pups' age and the difference in response between the mother
203 and the non-mother stimuli (PC scores mother – PC scores non-mother).

204 *Acoustic similarity between playback stimuli*

205 In order to measure the acoustic similarity between the two playback stimuli (filial and non-
206 filial pup calls; mother and non-mother calls), spectrograms of each of the 6 vocalizations (or less
207 depending on playback series) of the playback tracks were created (Hamming window, FFT size = 512,
208 frame size = 100%, overlap = 87.5 %) and spectrogram correlations were performed using Avisoft
209 Correlator function. The program compared spectrograms of all calls to each other and returned
210 correlation coefficients in a correlation matrix. Spectrogram correlations were made with a tolerate
211 frequency deviation of 10 Hz for females and 20 Hz for pups. These values were chosen based on the
212 intra-individual variation of the fundamental frequency (Martin et al. 2021a). Intra-individual acoustic
213 similarity was thus determined as the average of the intra-individual similarity scores. Inter-individual
214 acoustic similarity (i.e. between the two individuals used in an trial) was the average of the inter-
215 individual similarity scores. The relationship between the averaged inter-individual acoustic similarity
216 (%) and the difference in response between the two playback stimuli (PC scores filial – PC scores non-
217 filial or PC scores mother – PC scores non-mother) was investigated for both pups and mothers using a
218 linear regression. Statistical analyses were carried out using R (RStudio Version 1.4.1103, RStudio
219 Team 2021).

220 **Results**

221 The vocalisations of 44 females and 50 pups from marked mother-pup pairs were recorded. In total, 18
222 playback trials were initiated on females and 31 trials on pups.

223 **Mothers' response**

224 A total of 18 balanced playback trials were initiated on females but 7 were not included in the
225 dataset for one of three reasons: 1) only one series could be conducted because the focal female left (n
226 = 2), 2) the female was disturbed by another individual during the playback trial (n = 3) or 3) the female
227 did not respond to both stimuli (e.g. sleeping or unmotivated animals; n = 2). The final dataset therefore
228 consisted of 11 trials conducted on different females. Mean values (\pm standard error) of the five response
229 variables measured during the playback trials conducted on mothers are presented in Figure 1 (top

230 panel). Latencies to look, to move and to call were shorter during the filial stimulus while the look
231 duration and the number of calls were greater for the filial stimulus.

232 The PCA performed with the five behavioural variables extracted five principal components. A
233 summary of the first two PC is provided in Table 1. PC1 was the only component with an eigenvalue
234 greater than 1 (Table 1) and is therefore the one chosen to quantify the response of females to playbacks,
235 explaining 66.8 % of the total variance. Strong behavioural responses corresponded to negative values
236 of PC1 scores, and were characterised by short latencies (i.e. latency to look, to move or to call), long
237 period of looking towards the speaker during the broadcast and high number of calls produced in
238 response. In contrast, positive values of PC1 scores matched with little attention to the speaker, long
239 latencies and few calls produced (Table 1). We found significant differences between PC1 scores
240 obtained for filial and non-filial pups' calls: mothers' responses to their filial pup vocalizations were
241 significantly stronger (lower PC1 scores, Wilcoxon paired signed rank test, $n = 11$, $V = 64$, $p = 0.0029$)
242 in comparison to responses to playback of vocalizations from a non-filial pup (Figure 2).

243 Of the 11 trials, four mothers visually verified the presence of their pup on their side during the
244 filial playback. All females' checks were visual only as no female sniffed her pup to confirm its identity.
245 By comparing the reaction of the different females to the filial stimulus, it revealed that females who
246 did not check their pup showed significantly stronger behavioural responses (lower PC1 scores values)
247 to their pup's calls than those who actually looked at their filial pup (Wilcoxon rank sum test, $W = 2$, p
248 $= 0.0242$) (Figure 3).

249 Depending on female, pups' vocalizations were recorded 1 to 73 days prior to their mothers'
250 playback trial. No significant relationship was found between the mothers' response to the filial stimulus
251 and the time elapsed between the pup recording and the playback trial (*linear regression*, $F(1,9) = 2.28$,
252 $p = 0.1651$). The behavioural responses of females were not stronger when the time elapsed between
253 recording and testing was shorter.

254 **Pups' response**

255 A total of 31 playback trials were initiated on pups but 14 were not included in the dataset for
256 one of two reasons: 1) only one series could be conducted because the focal pup left ($n = 6$) or 2) the
257 pup did not respond to both stimuli, e.g. sleeping or unmotivated animals ($n = 8$). The final dataset
258 therefore consisted in 17 trials conducted on different pups. The age of 9 pups could be estimated based
259 on the date of their first marking and pups' ages ranged from 1- to 13-weeks old during recordings.

260 Mean values (\pm standard error) of the five response variables measured during the playback
261 trials conducted on pups are presented in Figure 1 (bottom panel). Similar to mothers, latencies to look,
262 to move and to call were shorter while the look duration and the number of calls were longer for the
263 filial stimulus. We reported a higher average number of calls produced by pups compared to females in
264 response to playback series. The PCA performed with the five behavioural variables also extracted five
265 principal components. The first two PCs (PC1 and PC2) - explaining a cumulative percentage of
266 variance of 75.7 % - were retained because they had eigenvalue greater than 1 (Table 1). Negative values
267 of PC1 scores corresponded to a short latency to move and a long period of looking towards the speaker
268 during the broadcast, indicating strong behavioural responses. Negative values of PC2 scores matched
269 with short latencies to look, but long latencies to call and few calls produced (Table 1). Negative values
270 of PC2 scores corresponded to strong behavioural responses, fast looking response but no or slow vocal
271 responses.

272 As with mothers, we found significant differences in the PC1 scores values between mother and
273 non-mother stimuli: pups' responses to their own mother vocalizations (mother stimulus) were
274 significantly stronger (lower PC1 scores, Wilcoxon paired signed rank test, $n = 17$, $V = 137$, $p = 0.0026$)
275 than those to non-affiliated females (non-mother stimulus), demonstrating that pups recognise the voice
276 of their mother (Figure 2). PC2 scores were not significantly different between mother and non-mother
277 stimuli (Wilcoxon paired signed rank test, $n = 17$, $V = 50$, $p = 0.2247$).

278 When looking at pups' response to their mother vocalizations as a function of their age
279 (estimated in weeks), we found lower responses (PC1 scores significantly increasing) when pups were
280 getting older (linear regression, $F(1,7) = 5.971$, $p = 0.0447$, adjusted $R^2 = 0.3828$) (Figure 4). The
281 difference in reaction between mother and non-mother stimuli (PC1 scores mother – PC1 scores non-

282 mother) showed a significant decrease with pups' age as well (linear regression, $F(1,7) = 6.949$, $p =$
283 0.0336 , adjusted $R^2 = 0.4265$) (Figure 4). Pups therefore displayed stronger behavioural responses to
284 their mother's vocalizations at a very young age and responded less strongly a few months after birth.

285 **Influence of acoustic similarity between stimuli**

286 Intra-individual acoustic similarity was measured for each playback track: females had a median
287 PAC acoustic similarity of 59.6 % (range 34.2 % to 81.6 %) and pups one of 52.5 % (range 33.2 % to
288 74.4 %, Figure 5). Inter-individual acoustic similarity as measured between calls of the two playback
289 series was assessed for each pair of stimuli. Inter-individual acoustic similarities in the PAC tracks
290 ranged between 15.3 % and 48 %. In FAC playback tracks inter-individual acoustic similarities ranged
291 between 5.8 % to 41.3 % (Figure 5).

292 The difference in behavioural responses between the two playback stimuli (PC1 scores filial
293 pup or mother - PC1 scores non-filial pup or non-mother) was investigated as a function of the acoustic
294 similarity between the two stimuli for both mothers and pups (Figure 6). Linear regressions revealed no
295 significant relationship between these two variables, meaning that the discrimination between the two
296 playback stimuli is the same regardless of the level of acoustic similarity between the two playback
297 tracks, for both mothers and pups (mothers: linear regression, $F(1,9) = 0.136$, $p = 0.7213$, adjusted $R^2 =$
298 -0.0946 , pups: linear regression, $F(1,15) = 0.588$, $p = 0.4551$, adjusted $R^2 = -0.0264$)

299 **Discussion**

300 The present study tested whether CFS females and pups use their individually specific calls to
301 recognize each other. Our playback experiment showed that mother-offspring vocal recognition occurs
302 in this species and is mutual. Such a mechanism is essential for this species where mother and pup are
303 regularly separated and must reunite in a noisy and confusing environment. As described by Bradbury
304 and Vehrencamp (1998), mother-offspring recognition partly depends on the mobility of the offspring
305 and the number of nearby non-offspring young. In highly dense colonies where pups can move around
306 during the absence of their mothers, the use of acoustic signals seems particularly well adapted to
307 facilitate mother-pup reunion. Indeed, vocal signals can propagate reliably over long distances, and are

308 therefore the most reliable signal when spatial cues are rare (i.e., no meeting place) and because visual
309 and olfactory cues are not effective at a long distance. Evidence that these sensory modalities (i.e. visual
310 and olfactory) can be used by mothers to recognize their pup has been found in Australian sea lion
311 (Pitcher et al. 2011; Wierucka et al. 2017). However, they might serve as a double-check when mother
312 and pup are in close contact (Charrier 2020; Pitcher et al. 2012; Stirling 1971)) and are thus part of a
313 multimodal identification process (Wierucka et al. 2018). Our findings also emphasized the importance
314 of a multimodal communication system between mother and young. Although all females were tested
315 in the presence of their pups, some females opted for a visual verification of their pup's presence when
316 they heard their pup's calls coming from an opposite side. These mothers then showed lower behavioral
317 responses to the playback series: they looked less insistently toward the speaker, they did not approach
318 the sound source, and they did not call back. These differences in females' behavioral response show
319 that they have different strategies to maintain the mother-pup bond. This may be related to differences
320 in personality, age or experience of females, with some being more protective and responsive to their
321 pup.

322 We demonstrate that mother-pup vocal recognition is mutual. These findings reinforce the idea
323 that pinniped species with moderate to high selective pressures for recognition have developed
324 adaptative and efficient mechanisms of recognition (Charrier 2020). This is consistent with previous
325 studies on otariids showing that recognition is mutual in species facing moderate to high ecological
326 constraints such as the Subantarctic fur seal (*Arctocephalus tropicalis*, Charrier et al. 2001a, 2002), the
327 Northern fur seal (*Callorhinus ursinus*, Insley 2001) and the Australian sea lion (*Neophoca cinerea*,
328 Charrier et al. 2009; Pitcher et al. 2012). The pup's ability to recognize its mother voice likely also
329 facilitates and greatly accelerates the reunion of the two individuals after a foraging trip at sea or after a
330 separation within the colony.

331 In Otariids, the recognition of the pup's voice by the mother must occur quickly after birth, as
332 females undertake their first foraging trip at sea a few days after parturition. In Australian sea lion,
333 females showed a clear ability to recognize their pup's voice within the first 48 hours after parturition
334 (Pitcher et al. 2010). In a colonial phocids, the Northern elephant seal, colonies are very large and

335 mothers and pups can be frequently separated due to conspecifics' movements. Northern elephant seal
336 females were also reported to recognize their pup's call within the first 24 hours of life (Linossier et al.
337 2021). Considering that the mothers first foraging trip at sea occurs on average 6 days after parturition,
338 it is more likely that such vocal recognition will be established within the first days of pup's life in CFS.
339 This individual recognition must be maintained throughout the entire lactation period and must therefore
340 be updated to include acoustic changes in the calls of the pups i.e. the new versions of pup's
341 vocalizations. Indeed, CFS pups' calls characteristics change over time during the lactation period such
342 as duration, fundamental frequency values, frequency modulation pattern and spectral features (Martin
343 et al. 2021a). In this study, females were tested with their pup's calls recorded several weeks prior to
344 the playback experiment and they still displayed strong behavioral responses to their filial pup's calls,
345 compared to non-filial pups. This suggest that CFS females were still able to recognize and remember
346 their pup's voice for at least several weeks (up to a maximum of 73 days in this study). Similar findings
347 have been reported in the Subantarctic fur seal where females memorized subsequent versions of their
348 pups' calls (Charrier et al. 2003a). As suggested in this study, such memorization process does not seem
349 to be advantageous for the species and could be only a by-product of the strong and 'unalterable' learning
350 capacity of females.

351 We performed playback trials on pups of different ages, between 1 to 13-week-old. Recognition
352 of the mother's PAC was found in all individuals, even the youngest ones. Further investigations on the
353 ontogeny of the vocal recognition by pups and mothers would be needed to assess precisely the timing
354 of such recognition onset. Based on our findings, pups are likely to develop the ability to recognize their
355 mother's voice within a few days after birth. This would be consistent with our current knowledge of
356 the ontogeny of mother-pup vocal recognition in Otariids. Indeed, in species showing the highest
357 ecological constraints, the recognition is established more rapidly (between 2 and 5 days in Subantarctic
358 fur seal, Charrier et al. 2001a) than for species with lower colony density: 10-30 days in Galapagos sea
359 lion (*Zalophus wollebaeki*, Trillmich 1981), 10 days in Galapagos fur seal (*Arctocephalus*
360 *galapagoensis*, Trillmich 1981) and between 10 days and 2 months in Australian sea lion (Pitcher et al.
361 2009). Furthermore, we found a significant decrease in pups' response to their mother's calls with age.

362 When getting older, pups still discriminated their mother's voice from those of other females, but they
363 showed a weaker behavioral response i.e. they were looking less towards the speaker and they had a less
364 intense searching behavior. However, their responses to non-mother vocalizations were stable and
365 always weak. We can suggest multiple reasons for this decrease in pup's behavioral response with age,
366 but also for the number of aborted playback trials in pups. First, there might be a decrease in dependence
367 on the mother due to a decrease in the need for food and/or protection as pups grow. This is also
368 associated with an increase in the duration of mothers' foraging trips at sea (David and Rand 1986).
369 Secondly, structural changes in the colony at the end of the breeding season may affect the behavior and
370 responsiveness of the pups. From January, when the pups are about 2 months old, adult males leave the
371 colony to feed at sea and the harem structure of the breeding season breaks up. Pups form large crèches
372 in which they gather during their mother's absence. During this period, they are more mobile, show more
373 interactions with other pups and seem to show less attention to their mother's calls. Compared to other
374 fur seal species for which the mothers can stay at sea for 2 to 3 weeks (Georges and Guinet 2000), CFS
375 mothers remain in regular attendance and generally alternate onshore nursing period (1.9 days) with
376 offshore foraging trip (5.2 days) (Kirkman and Arnould 2018). The mothers' foraging trip in CFS being
377 quite short, the pups' nutritional resources are not depleted and thus their motivation to reunite with their
378 returning mother may be lower. Pups' responsiveness and selectiveness have been shown to vary during
379 mother's absence in Subantarctic fur seals (Charrier et al. 2002a). Indeed, in this species, the longer the
380 mother has been absent at sea, the higher the probability of the pup to respond to the calls of a stranger
381 female. This decrease in the selectivity of the pup to respond to its mother compared to other a stranger
382 female over time when the mother is at sea can be explained by an increasing motivation of the pup to
383 beg for food.

384 The individual vocal recognition modalities of a species depends above all on its auditory
385 abilities and cognitive abilities to process the information (Yorzinski 2017). In this study, we found that
386 both mothers and pups could discriminate between acoustically similar vocal stimuli in order to
387 discriminate the calls of their filial pup's calls or mother's calls. These results are consistent with previous
388 studies on individual vocal signature in pinnipeds, showing that small modifications in females or pups'

389 calls can inhibit individual recognition. For instance, Subantarctic fur seal (*Arctocephalus tropicalis*)
390 pups are sensitive to a -100 Hz shift in their mother's calls (Charrier et al. 2003b). In the Australian sea
391 lion (*Neophoca cinerea*), pups do not respond to their mother's calls in which the absolute frequency
392 values were increased by 75 Hz (Pitcher et al. 2012). The present results in Cape fur seals revealed that
393 the communication system of this species appeared to be well adapted to an extremely colonial life.
394 Their perceptual abilities seem to be highly performant and allow for slight detection of acoustic
395 variations among calls produced by hundreds of conspecifics constantly surrounding them. This
396 adaptation is a response to the high risk of confusion between individuals in the crowded colony. In
397 addition, the rarity of allo-suckling in Cape fur seal (Rand 1955) is likely to strengthen the bond between
398 mother and pup in CFS and serve as a selection pressure for individual recognition. Their ability to
399 recognize each other and quickly reunite is crucial to the pup's survival and female's reproductive
400 success. To reduce the energy cost to the female and to ensure the nursing of the young, their reunion
401 after a foraging trip at sea must be accurate and quick.

402

403

Conclusion

404 To conclude, our study demonstrates the first evidence of mutual vocal recognition between
405 mother and pup in Cape fur seals. Females memorize and recognize their pup's voice and recall previous
406 versions of their pup's calls for several weeks at least. Pups discriminate their mother's voice from others
407 at least one week after birth and they showed a decrease in responsiveness to their mother's calls with
408 age. Finally, both females and pups developed fine abilities to perceive acoustic differences among the
409 numerous signals produced within the colony and thus to differentiate between vocalizations of high
410 similarity. Further investigations on both the onset time of mother-pup vocal recognition and the
411 individual vocal signature are now needed for a better understanding of mother-pup communication
412 strategy of the extremely colonial Cape fur seal.

Tables

Table 1 Summary of the first two principal components (PC1 and PC2) resulting from the two principal component analysis (PCA) performed on mothers and pups' playback trials with five behavioural variables

	Playbacks on mothers		Playbacks on pups	
	PC1	PC2	PC1	PC2
Eigenvalues	3.34	0.96	2.10	1.68
% cumulative variance	66.79	85.95	41.99	75.68
Correlation coefficients between PC and variables				
Latency to look	0.67	0.68	0.63	0.65
Look duration	-0.90	-0.35	-0.75	-0.50
Latency to move or posture change	0.76	-0.04	0.64	0.11
Latency to call	0.85	-0.44	0.62	-0.70
Number of calls	-0.89	0.41	-0.59	0.71

Figures captions

Fig. 1 Response variables measured during the playback experiment conducted on mothers and pups (mean \pm standard error; $n=11$ mothers and 17 pups): latency to look (abbreviated as LL), look duration (LD), latency to move (LM), latency to call (LC), and number of calls (NC).

Fig. 2 Behavioural response of mothers to filial and non-filial stimuli (indicated by PC1 scores) and behavioural response of pups to mother and non-mother stimuli (indicated by PC1 scores). Statistical test: Wilcoxon paired signed rank test: $V = 64$, $p = 0.0029$ for mothers and $V = 137$, $p = 0.0026$ for pups. Y axis is reversed because highly negative PC1 scores values correspond to a strong behavioural response. Boxplots present median values with first and third quartiles (lower and upper hinges) and interval between the smallest and the largest values (whiskers, no further than $1.5 \times \text{IQR}$ from the hinge).

Fig. 3 Behavioural response of mothers to the filial stimulus (vocalizations of their own pup, indicated by PC1 scores filial) depending on whether they visually checked the presence of their pup nearby during the experiment, or not. Statistical test: Wilcoxon rank sum test: $W = 2$, $p = 0.0242$. Y axis is reversed because highly negative PC1 scores values correspond to a strong behavioural response. Boxplots present median values with first and third quartiles (lower and upper hinges) and interval between the smallest and the largest values (whiskers, no further than $1.5 \times \text{IQR}$ from the hinge).

Fig. 4 Relationship between behavioural response of pups to the mother stimulus (vocalizations of their own mother, indicated by PC1 scores mother – *black axis*) or difference in response between mother and non-mother stimuli (indicated by PC1 scores mother – PC1 scores non-mother – *blue axis*) and pups' age in weeks. PC1 scores mother axis (black) is reversed because highly negative PC1 scores values correspond to a strong behavioural response.

Fig. 5 Spectrograms of four playback tracks composed of pups' calls: Averaged intra-individual acoustic similarity: 63 % for a1, 55.9 % for a2, 74.4 % for b1 and 42.1 % for b2. Averaged inter-individual acoustic similarity between the calls of pair a (tracks a1 and a2) was 41.3 % while the calls of pair b (tracks b1 and b2) it is 5.8 %. The inter-call interval was reduced from 3 s on the original tracks to 0.5 s for a better visualization.

Fig. 6 Relationship between the difference in response between the two playback tracks (indicated by PC1 scores filial – PC1 scores non-filial for mothers, and PC1 scores mother – PC1 scores non-mother

for pups) and the percentage of acoustic similarity between the two playback stimuli for both mothers' and pups' playback trials. None of them showed a significant correlation (p-values > 0.4).

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Declarations

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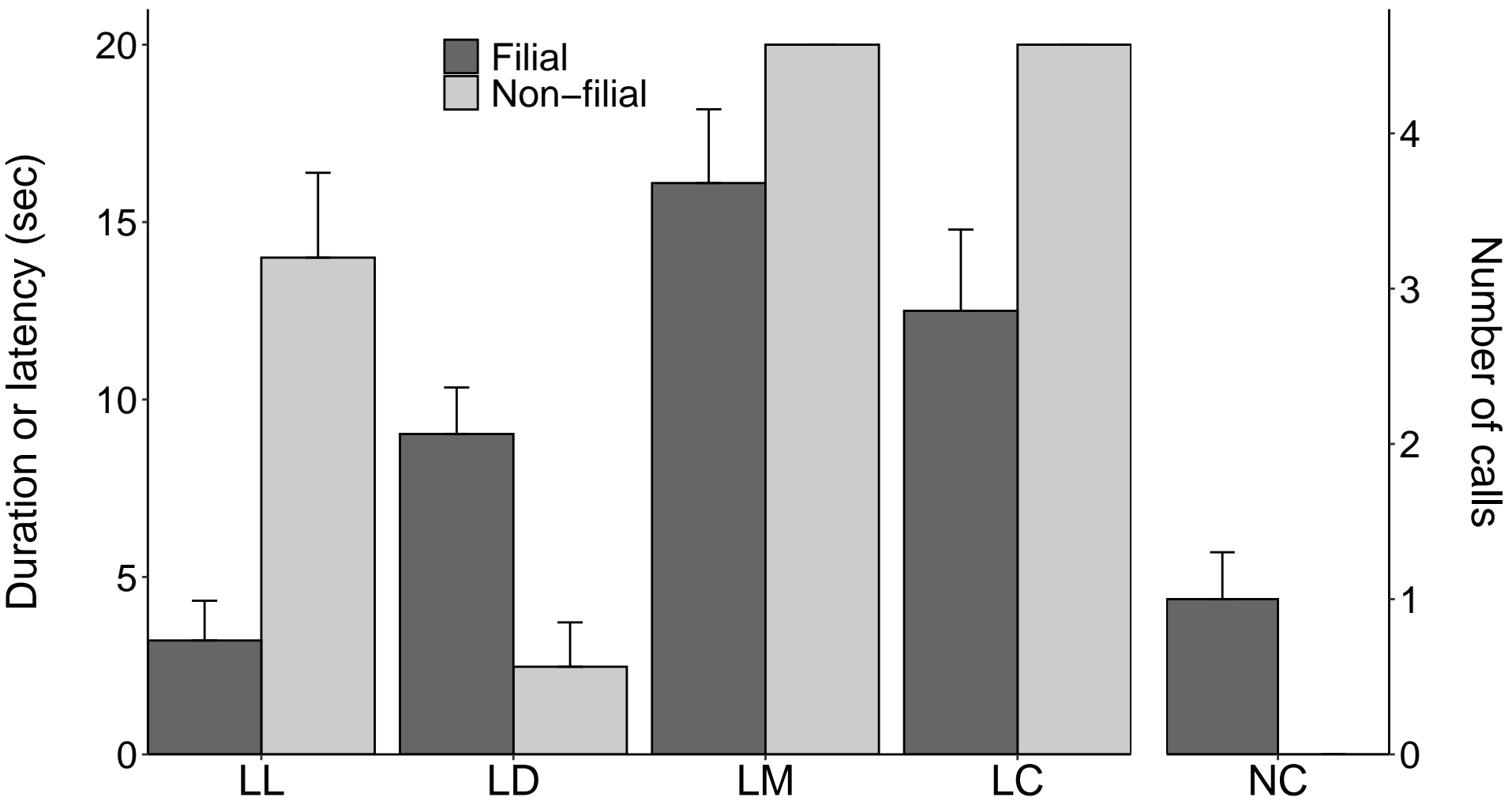
Competing interests: We have no competing interests.

Availability of data: Data for this paper are deposited in the Zenodo repository (<http://doi.org/10.5281/zenodo.4630682>).

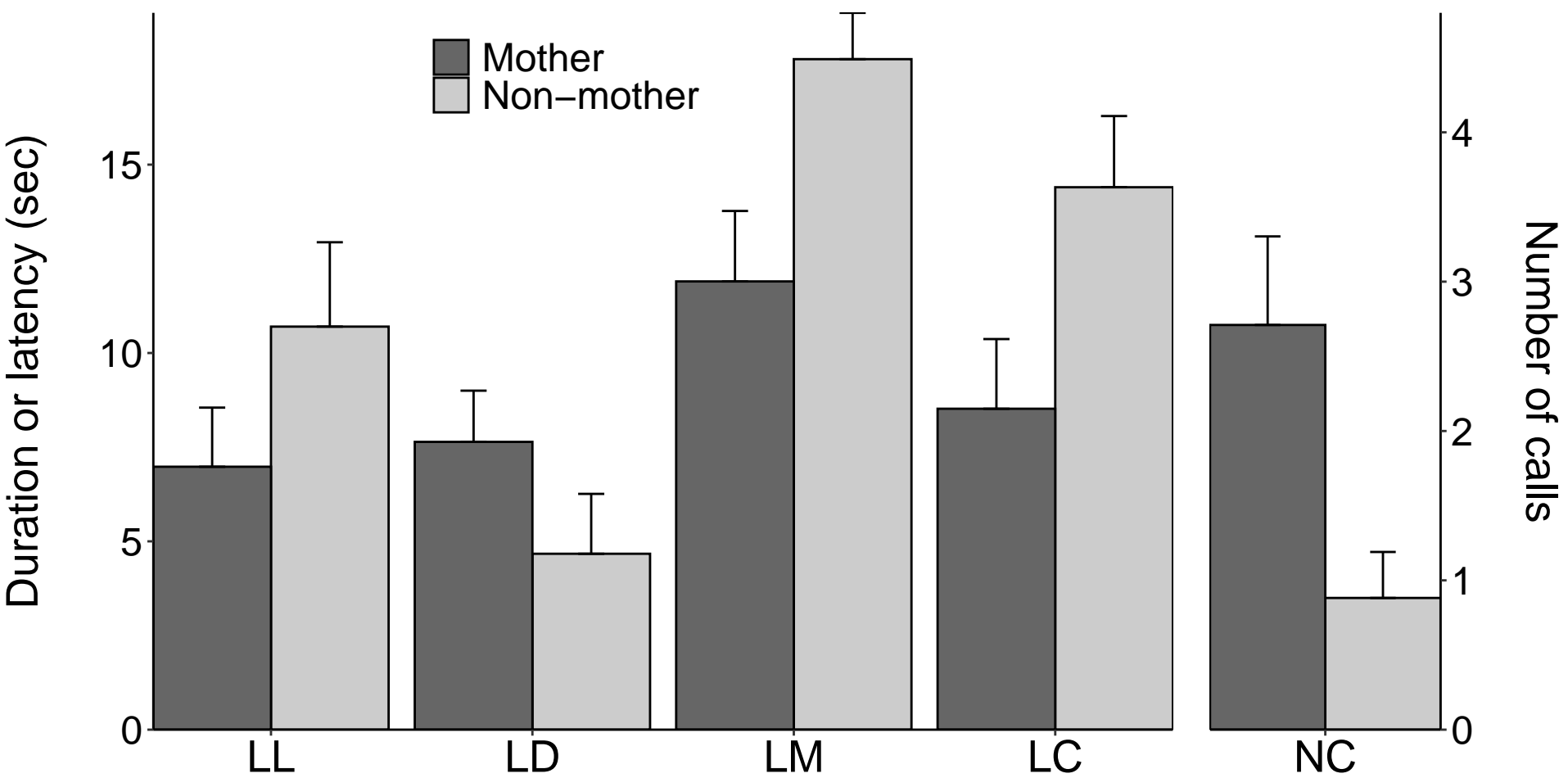
Authors' contributions: I.C and M.M designed the study. I.C, T.G and S.H.E organised the fieldwork logistics. M.M and D.F collected the data. M.M analysed the data. M.M and I. C drafted the manuscript, and all authors revised the manuscript.

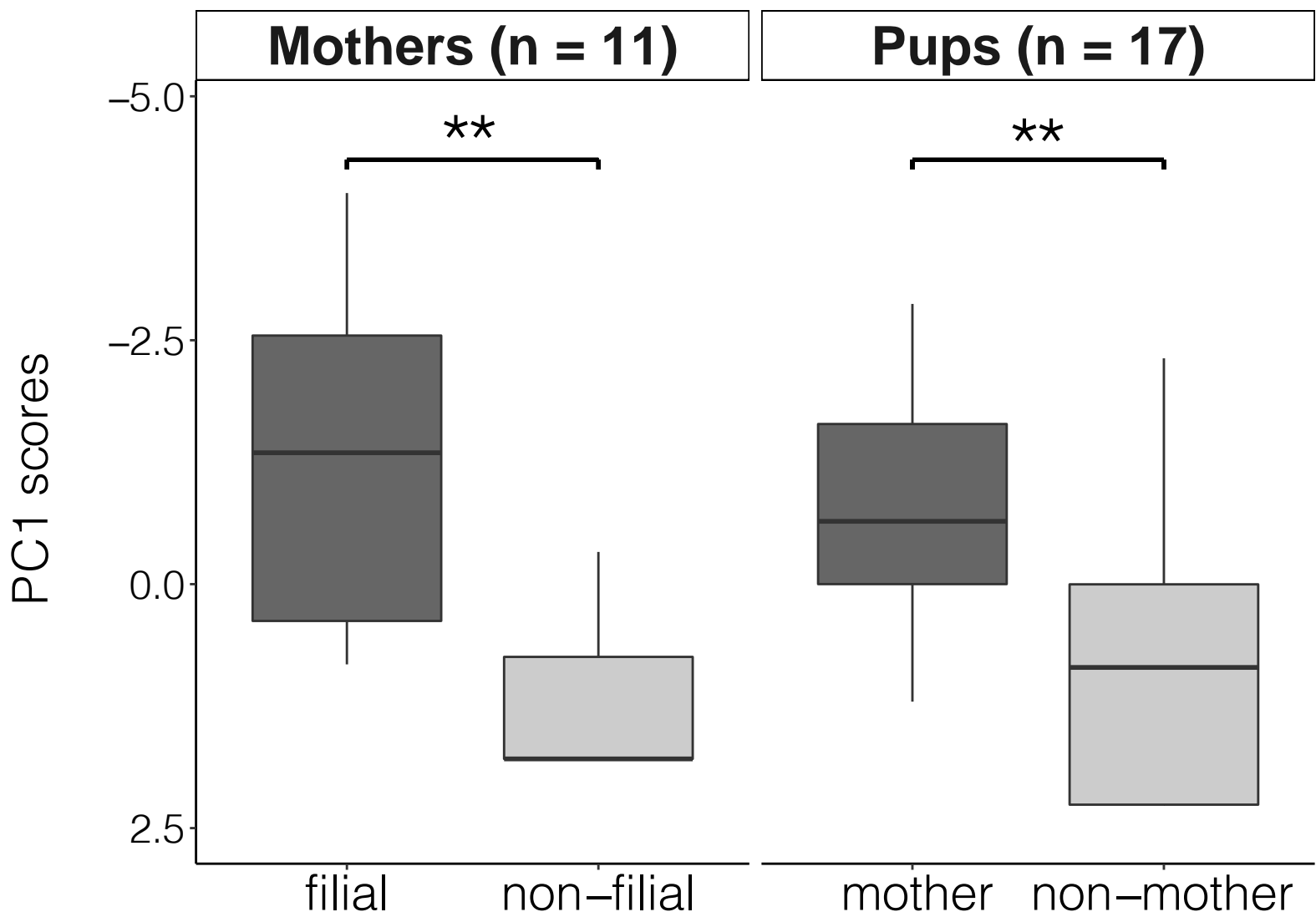
Ethics approval: This present study complies with the European Union Directive on the Protection of Animals Used for Scientific Purposes (EU Directive 2010/63/EU) and with current Namibian laws. Fieldwork was permitted by the Namibian Ministry of Fisheries and Marine Resources (MFMR).

Mothers

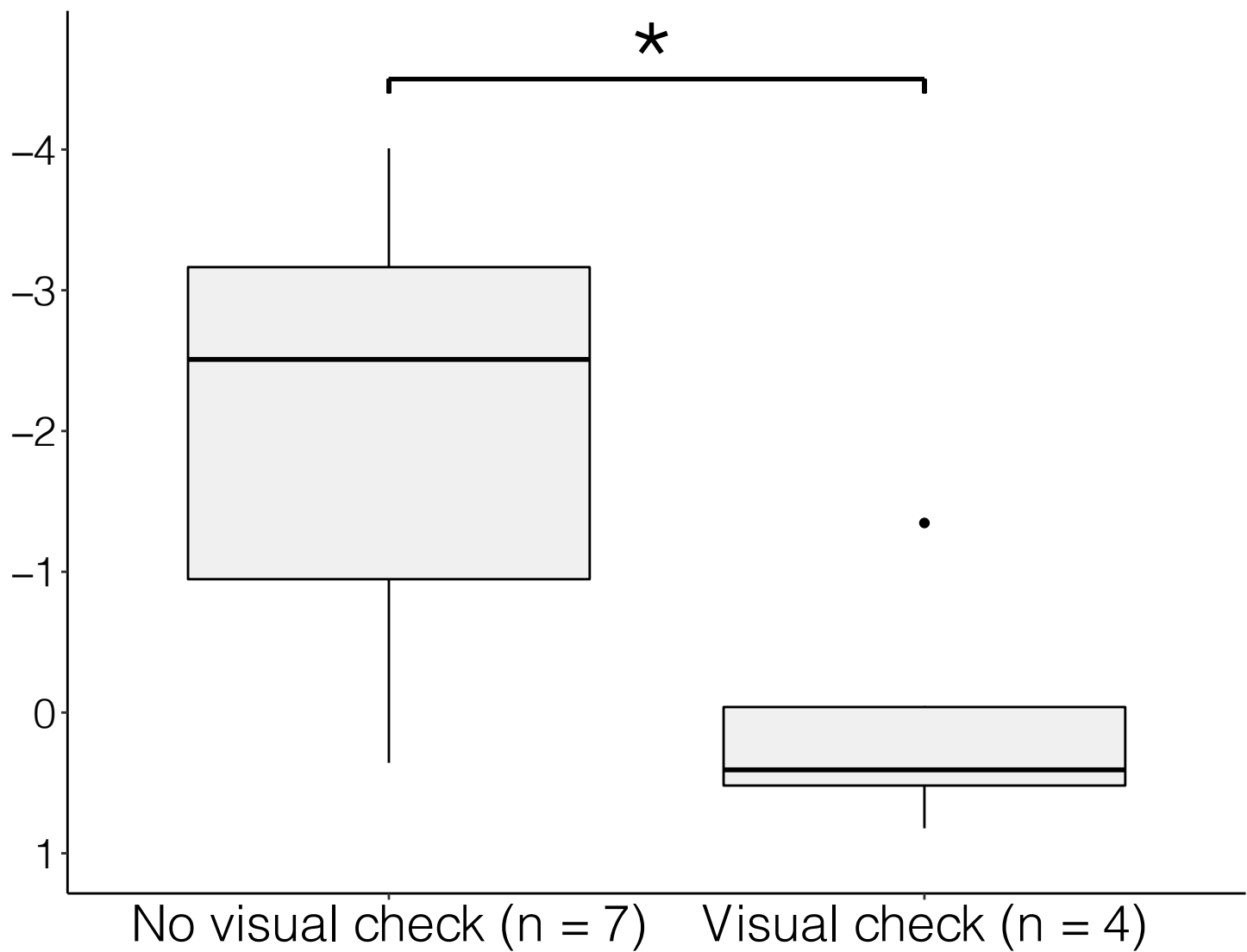


Pups

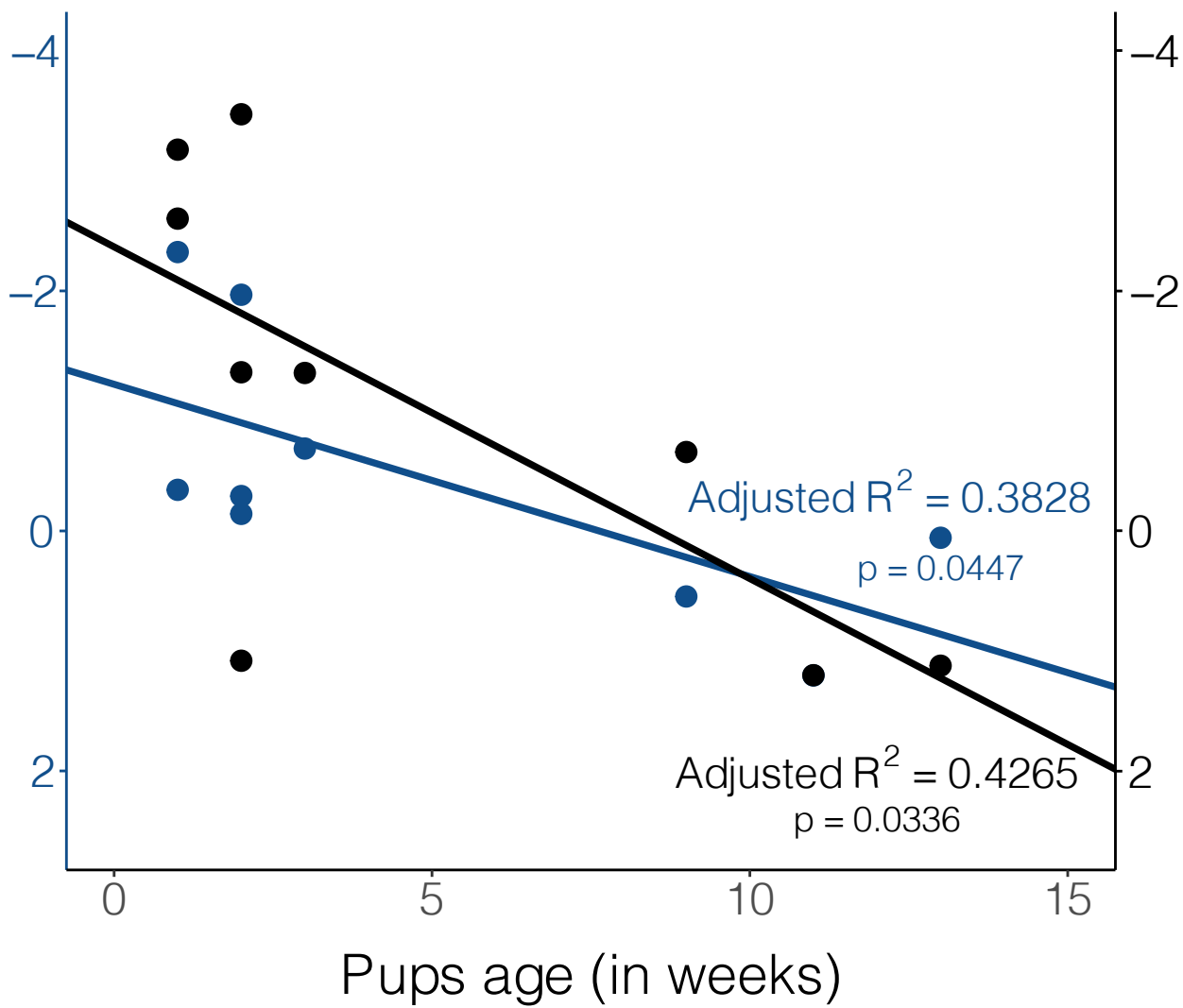




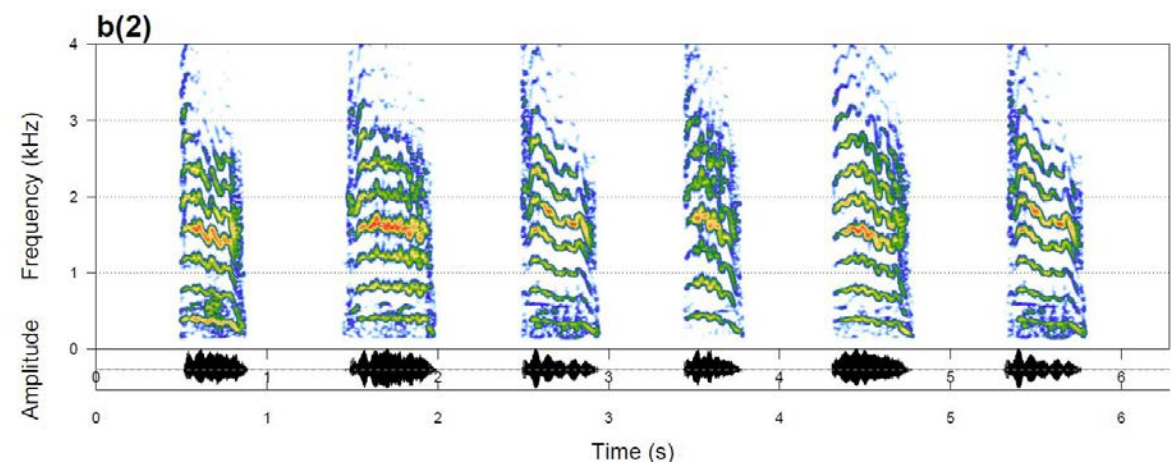
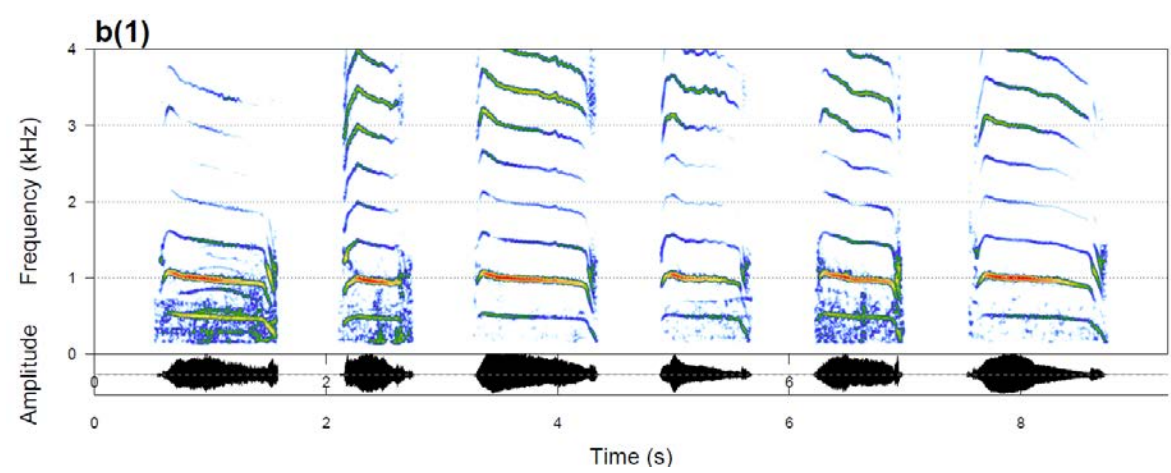
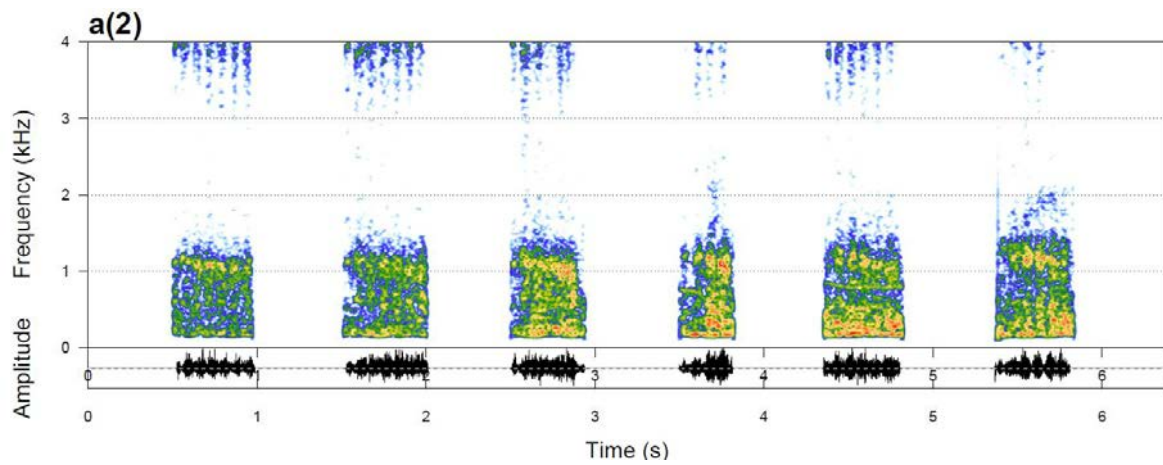
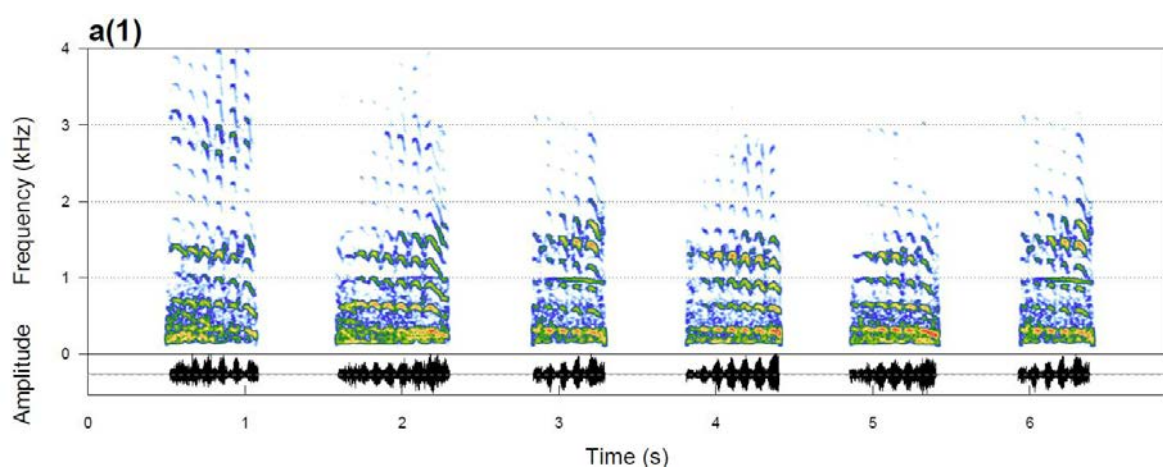
PC1 scores filial



PC1 scores mother

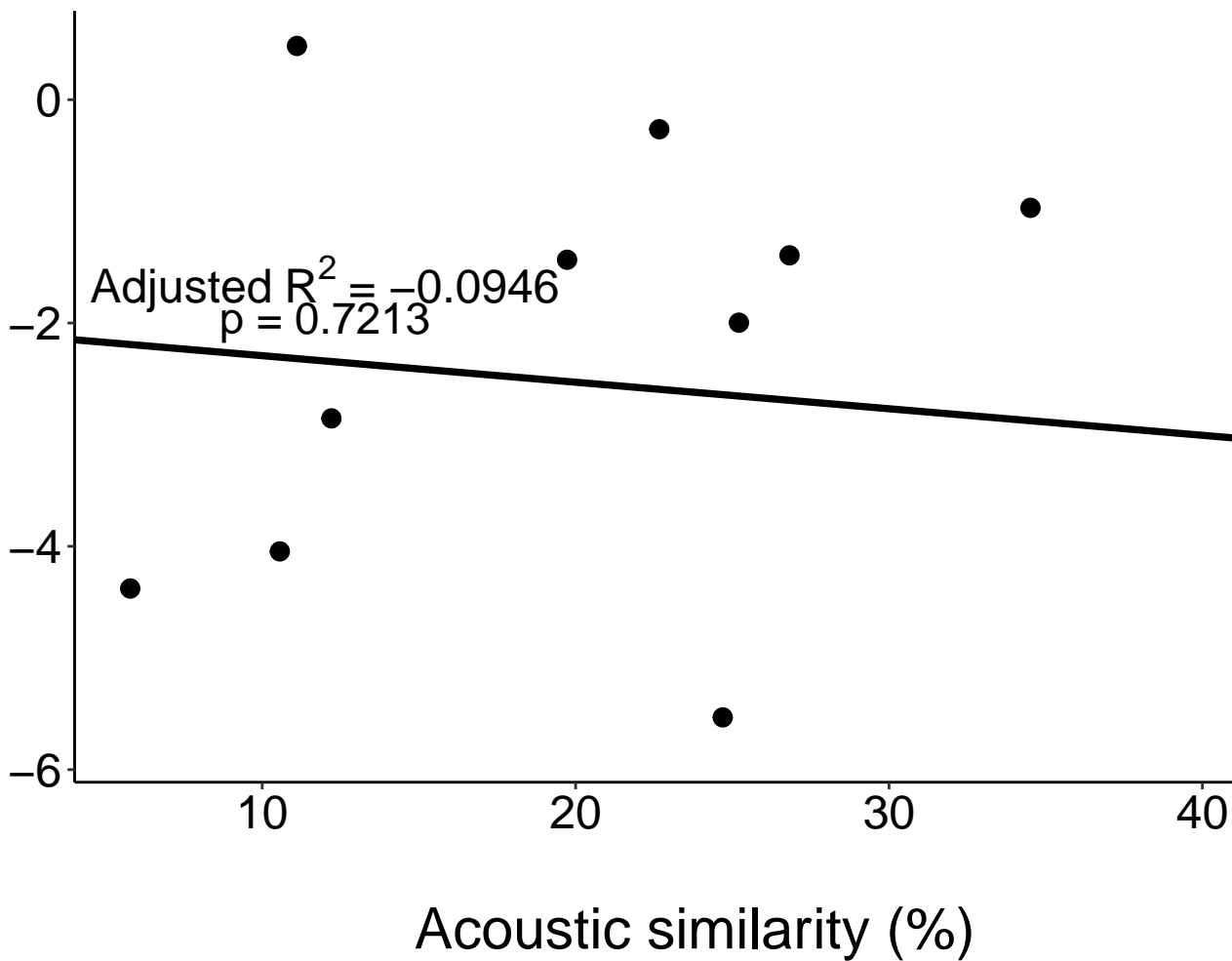


PC1 scores mother - PC1 scores
non-mother



Mothers

PC1 scores filial – PC1 scores
non–filial



Pups

PC1 scores mother – PC1 scores
non–mother

