



HAL
open science

Extreme ecological constraints lead to high degree of individual stereotypy in the vocal repertoire of the Cape fur seal (*Arctocephalus pusillus pusillus*)

Mathilde Martin, Tess Gridley, Simon Elwen, Isabelle Charrier

► To cite this version:

Mathilde Martin, Tess Gridley, Simon Elwen, Isabelle Charrier. Extreme ecological constraints lead to high degree of individual stereotypy in the vocal repertoire of the Cape fur seal (*Arctocephalus pusillus pusillus*). *Behavioral Ecology and Sociobiology*, 2021, 75 (7), pp.104. 10.1007/s00265-021-03043-y . hal-03331444

HAL Id: hal-03331444

<https://hal.science/hal-03331444>

Submitted on 8 Oct 2021

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

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

Behavioral Ecology and Sociobiology

Extreme ecological constraints lead to high degree of individual stereotypy in the vocal repertoire of the Cape fur seal (*Arctocephalus pusillus pusillus*)

--Manuscript Draft--

Manuscript Number:	
Full Title:	Extreme ecological constraints lead to high degree of individual stereotypy in the vocal repertoire of the Cape fur seal (<i>Arctocephalus pusillus pusillus</i>)
Article Type:	Original Article
Corresponding Author:	Mathilde Martin, M.D. Institut des Neurosciences Paris-Saclay FRANCE
Order of Authors:	Mathilde Martin, M.D. Tess Gridley Simon Elwen Isabelle Charrier
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Institut des Neurosciences Paris-Saclay
Corresponding Author's Secondary Institution:	
First Author:	Mathilde Martin, M.D.
First Author Secondary Information:	
Order of Authors Secondary Information:	
Funding Information:	
Abstract:	<p>The ability to recognize the identity of conspecifics is a key component for survival of many animal species and is fundamental to social interactions such as parental care, intra-sexual competition or mate recognition. In group-living species, the simultaneous co-existence of many individuals increases the number of interactions and reinforces the need for individual recognition. Acoustic signals are widely used by birds and mammals to communicate and to convey information about identity, but their use in very dense colonies becomes challenging due to the high level of background noise and the high risk of confusion among individuals. The Cape fur seal (CFS) is the most colonial pinniped species and one of the most colonial mammals in the world, with colonies of up to 210,000 individuals during the breeding season. Here, we investigated the individual stereotypy in vocalizations produced by pups, females and male CFS using Random Forests and index of vocal stereotypy (IVS). We thus compared IVS values of CFS to other pinniped species. Within CFS we identified individuality in all call types but the degree of individual stereotypy varies in regards to their social function: affiliative calls produced in a mother-pup reunion context and territorial calls produced by mature bulls holding harem were more individualized than vocalizations involved in agonistic interactions. Our inter-species comparisons among pinnipeds showed that CFS affiliative and territorial calls displayed higher degrees of individuality compared to other species with similar or lower ecological constraints (colony density and social structure).</p>
Suggested Reviewers:	Charlotte Curé charlotte.cure@cerema.fr expert in marine mammal vocal communication and vocal signatures Elodie Briefer elodie.briefer@bio.ku.dk expert in mammal vocal communication and vocal signatures

	Benjamin Charlton bencharlton829@gmail.com expert in mammal vocal communication
	Renata Sousa-Lima lab.bio.br@gmail.com expert in marine mammal vocal communication
	Dan Blumstein marmots@ucla.edu expert in mammal vocal communication
	Sofie Van Parijs sofie.vanparijs@noaa.gov expert in mammal vocal communication
Opposed Reviewers:	

[Click here to view linked References](#)

Mathilde Martin^{a,b}, Tess Gridley^{b,c}, Simon Harvey Elwen^{b,c}, Isabelle Charrier^a

**Extreme ecological constraints lead to high degree of individual
stereotypy in the vocal repertoire of the Cape fur seal
(*Arctocephalus pusillus pusillus*)**

^a Université Paris-Saclay, Université Paris-Sud, CNRS, UMR 9197, Institut des Neurosciences Paris-Saclay, 91405 Orsay, France.

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

^c Department of Botany and Zoology, Faculty of Science, Stellenbosch University, Stellenbosch, 7605, South Africa

corresponding author:

M. Martin, Equipe Communications Acoustiques, Neuro-PSI, CNRS UMR 9197, Université, Paris Sud, Orsay,

France. E-mail address: mathilde.martin@u-psud.fr

Abstract

The ability to recognize the identity of conspecifics is a key component for survival of many animal species and is fundamental to social interactions such as parental care, intra-sexual competition or mate recognition. In group-living species, the simultaneous co-existence of many individuals increases the number of interactions and reinforces the need for individual recognition. Acoustic signals are widely used by birds and mammals to communicate and to convey information about identity, but their use in very dense colonies becomes challenging due to the high level of background noise and the high risk of confusion among individuals. The Cape fur seal (CFS) is the most colonial pinniped species and one of the most colonial mammals in the world, with colonies of up to 210,000 individuals during the breeding season. Here, we investigated the individual stereotypy in vocalizations produced by pups, females and male CFS using Random Forests and index of vocal stereotypy (IVS). We thus compared IVS values of CFS to other pinniped species. Within CFS we identified individuality in all call types but the degree of individual stereotypy varies in regards to their social function: affiliative calls produced in a mother-pup reunion context and territorial calls produced by mature bulls holding harem were more individualized than vocalizations involved in agonistic interactions. Our inter-species comparisons among pinnipeds showed that CFS affiliative and territorial calls displayed higher degrees of individuality compared to other species with similar or lower ecological constraints (colony density and social structure).

Keywords

acoustic communication, Cape fur seal, individual recognition, vocal stereotypy, ecological constraints, colonial species

Significance statement

Individual recognition is primordial for the establishment of social interactions and notably occurs through acoustic signals in many birds and mammals species. Understanding the role of social complexity in the development of individual vocal recognition improves our general knowledge on acoustic communication in a social system. This study investigated the vocal stereotypy in the Cape fur seal (CFS), a species that is an extreme illustration of social complexity. The CFS is the most colonial pinniped species and this results in high selective pressure for individual recognition during mother-pup reunions and male territorial behaviour. By comparing the degree of individuality

contained in CFS vocalizations with other pinniped species, we can assess how ecological (environmental and social) constraints drive communication systems in vertebrates.

Declarations

Funding: The research was supported by CNRS and the Sea Search - Namibian Dolphin Project. This project has received financial support from the CNRS through the MITI interdisciplinary programs. . MM is funded by a PhD scholarship from the French Ministry of Higher Education and Research. TG was awarded by a post-doctoral fellowship from the University of Stellenbosch.

Conflicts of interest: We have no competing interests.

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 (include appropriate statements): All authors consent to participate.

Consent for publication (include appropriate statements): All authors consent to publish this work.

Availability of data and material (data transparency): Data for this paper are deposited in the Zenodo repository (10.5281/zenodo.4428112).

Code availability (software application or custom code): R scripts can be made available on reasonable request at the corresponding author.

Authors' contributions: I.C 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.

Acknowledgments

We acknowledge the Namibian Ministry of Fisheries and Marine Resources and the Namibian Chamber of Environment for their support of this research. We thank Dorothy Fourie for her assistance in the field. Special thanks to Naude Dreyer, Kevin van Schalkwyk, Craig Gibson and Jean-Paul Roux for their knowledge on the species, logistical support in the field, and their enthusiasm for the project.

Introduction

Individual recognition is defined as the process by which one individual is able to identify another from its distinctive characteristics (Sherman et al. 1997). It is a key component in all social behaviours and occurs in a wide range of intra-specific social interactions: parental care, sexual competition, territoriality, mate selection or kin recognition (Halliday and Slater 1983). In all cases, recognition benefits the sender and/or the receiver and represents a central factor for survival, reproductive success and fitness of individuals at all ages (Ward and Webster 2016). The study of social recognition is therefore fundamental to our understanding of animal social behaviour. Generally, the ability to identify a conspecific is related to both the ecology and the social structure of a given species. Although the notion of social complexity is difficult to define because it involves a large number of parameters (group/colony size, diversity of demographic roles, female gregariousness, grooming time or social affiliative value of the context, etc. ; Peckre, Kappeler, & Fichtel, 2019), species exhibiting complex or elaborated social lives generally have advanced recognition abilities (Ward and Webster 2016). In group-living species, social complexity is related to the size of social groups and the types of social interactions among group members, with bonded relationships (alliance, hierarchy) adding another layer in the social complexity (Freeberg et al. 2012). In these gregarious species, social interactions are complicated by the simultaneous co-existence of many individuals (Aubin and Jouventin 1998): animals frequently interact with many different individuals in a variety of social contexts. It is therefore crucial that animals are able to accurately identify surrounding conspecifics to be able to adjust their behavioural responses accordingly, with the aim of limiting interactions to relevant situations only (Knörnschild et al. 2020). An understanding of individual recognition processes in these socially complex species would improve our ability to decipher communication strategies in animal species.

Living in a colony results in strong constraints for communication. In a dense colony, many individuals may use the same sensory channels to communicate simultaneously and individuals can act as physical barriers for the propagation of any sensorial signals (Aubin and Jouventin 2002). Among the variety of sensory modalities used to communicate information about individual identity (visual, olfactory and auditory cues), acoustic signals are particularly effective as they allow rapid transmission

28 of a wide range of information, are easily localised and travel over long distances with little attenuation,
29 especially in marine habitats. Acoustic signals convey identity information and play a role in individual
30 recognition in several colonial species including seabirds (Robisson et al. 1993; Mathevon 1997;
31 Lengagne et al. 1999; Charrier et al. 2001c), bats (Wilkinson 2003; Carter et al. 2012) and pinnipeds
32 (seals, fur seals, sea lions and walrus - for reviews see Insley, Phillips, & Charrier, 2003; Charrier 2020).
33 However, within constraining environments such as very dense colonies, acoustic communication
34 becomes challenging due to a high level of background noise and a risk of confusion among individuals.

35 Pinnipeds are a mammalian clade showing a great diversity in both their social structures (from
36 solitary to highly colonial species) and mating systems (serial monogamy to high polygyny), and most
37 Otariids species (eared seals) show high selective pressures for individual recognition (Insley et al.
38 2003). During the breeding season, otariid species typically form large colonies and females nurse their
39 single pup while regularly foraging at sea for a few days at a time (Riedman 1990). Mother–young
40 recognition is therefore crucial for pup survival and for female breeding success as it avoids misdirected
41 maternal care and limits energy expenditure (Charrier et al. 2009). Recognizing specific individuals is
42 challenging for animals that are often separated in such large colonies but stereotypy of vocalizations
43 produced by mother and pup, and their role in recognition has been widely reported among Otariids
44 (Stirling 1971; Stirling and Warneke 1971; Trillmich 1981; Insley 1992; Fernández-Juricic et al. 1999;
45 Phillips and Stirling 2000; Charrier et al. 2002, 2003; Page et al. 2002; Tripovich et al. 2009, 2006).

46 Most studies have focused on individuality in mother-offspring pairs. However, a few studies
47 have also demonstrated that territorial males can recognize each other through their acoustic signals
48 (Stirling 1971; Roux and Jouventin 1987; Fernández-Juricic et al. 1999; Phillips and Stirling 2001).
49 Otariids species display moderate to high degrees of polygyny: territorial bulls defend their harem (or
50 mate-guarding males defend one or two females) through aggressive behaviours against neighbouring
51 or unfamiliar rivals. Territoriality can thus have important costs for males as they expend a lot of energy
52 while signalling, chasing, and fighting with rivals, in addition to the risks of injury (Bradbury and
53 Vehrencamp 2011). As neighbours may not necessarily constitute a serious threat to adjacent territory
54 holders, individual recognition of their close neighbours could allow harem holders to limit these costs

55 ('dear enemy effect'; Fisher, 1954). Individual recognition among males can thus be essential in a
56 context of competition for the establishment of territory and its maintenance.

57 Interestingly, there is a total lack of information about vocal communication in one the most
58 emblematic and colonial otariids species: the Cape fur seal *Arctocephalus pusillus pusillus* (CFS). As
59 one of the most colonial mammals in the world, this species is an extreme illustration for colonial
60 species, with colonies of several hundreds of thousands of individuals forming during the breeding
61 season (210,000 annually at Cape Cross seal reserve in Namibia (Ministry of Environment and Tourism,
62 <https://www.met.gov.na/national-parks/cape-cross-seal-reserve/214/>)). Breeding takes place from mid-
63 October to early January (Rand 1967; De Villiers and Roux 1992)), and at the beginning of the breeding
64 season, socially mature males (9-12 years old) establish territories and form harems monopolising 10 to
65 30 females (Wickens and York 1997). Females give birth to a single pup each year and exclusively nurse
66 their own young. Like all otariids species, the lactation period is long (weaning occurs around 9 to 11
67 months, David et al. 1986) and interspersed with maternal attendance periods on shore and foraging
68 trips at sea. In CFS, the first mother's first departure to sea typically occurs 6 days after parturition
69 (David et al. 1986) and females are absent for approximately 70% of the time until weaning (Gamel et
70 al. 2005). Like other pinniped species, Cape fur seals produce a diverse repertoire of vocalizations in
71 different social contexts: mother-young relationships (reunion and interaction), territorial defence and
72 mate selection. The social structure of Cape fur seals and the extreme size and density of colonies act as
73 strong selective pressures for individual recognition.

74 Here we investigated and compared individuality in the vocal repertoires of CFS individuals of
75 different sex, age and social roles. The first goal was to evaluate and compare the relative degree of
76 individuality in five call types commonly produced by Cape fur seals (intra-species comparison) studied
77 at two locations/colonies: Pelican Point and Cape Cross. Previous studies on birds (Charrier, Jouventin,
78 *et al.*, 2001; Mathevon, Charrier and Jouventin, 2003), primates (Mitani, Gros-Louis and Macedonia,
79 1996; Leliveld, Scheumann and Zimmermann, 2011) and canids (Déaux et al. 2016) have demonstrated
80 that individual distinctiveness depends on call function. Considering this, we hypothesized that the
81 degree of individuality might be variable among call types, with vocalizations involved in individual-
82 specific interactions (i.e. affiliative and territorial calls), being the most individualized. Calls produced

83 by pups were also analysed by age class (from less than 24 hours to 2-4 months) to investigate the
84 ontogeny of the individuality. As the topography of our two study sites was quite different, flat sandy
85 beach vs steep and rocky area, we postulated that the absence of spatial cues in a colony may increase
86 the difficulty of females to reunite with their pup when returning from foraging at sea. Indeed, otariid
87 mothers often return to their last suckling spot to reunite with their pup (Riedman 1990), but without
88 landmark, the task become harder. Such additional environmental constraints may thus increase the
89 degree of individuality in the vocalisations at different colonies. Therefore, the second objective was to
90 compare vocal stereotypy between two colonies with different physical environments. Finally, we
91 compare our results on Cape fur seals to other pinnipeds in an inter-species comparison of individual
92 vocal stereotypy (IVS). Considering the extremely constraining ecological environment, Cape fur seals'
93 vocal signals are likely to display a higher degree of individuality in their calls compared to species with
94 lower constraints for acoustic communication (Charrier 2020).

95

96

Methods

97 Study area

98 The study was conducted during and in the period immediately following the Cape fur seal breeding
99 season from mid-November 2019 to late-February 2020. Seals' vocalizations were recorded in two
100 breeding colonies located on the central Namibian coast: Pelican Point (25°52.2'S, 14°26.6'E) and Cape
101 Cross (21°46.5'S, 13°57.0'E). Established before the 20th century (Kirkman 2010), Cape Cross hosts
102 the world's largest breeding colony of CFS (and of pinnipeds) with about 210,000 individuals (Ministry
103 of Environment and Tourism). The Cape Cross colony expands over in a wide rocky bay with steep
104 topography. A pedestrian walkway for touristic viewing and an associated parking bay are located on
105 the inland edge of the colony. Pelican Point is a dynamic sandy peninsular with uniform, flat topography,
106 no rocks and only man made topographic cues (a jetty, lighthouse, and shipwreck). Most seals (and all
107 research) occur in the ~3km from the lighthouse to the northern tip, on both the bay and open-ocean side
108 of the point. The CFS colony at Pelican Point is a relatively recent and emerging colony (established

109 late 1990's) where pup production is increasing each year with up to 12,000 pups estimated at the last
110 aerial census in 2011 (MFMR unpubl. data).

111

112 **Animal identification**

113 *Pelican Point* - To keep track of individuals during recordings and to enable later identification to
114 perform playback experiments, pups were bleach-marked (hair dye: Blonde high-light kit, ©Kair) with
115 a number on the flank. We used a 10-cm wide wooden pad attached to the end of a 5-metre pole to work
116 at a distance and avoid disturbance of neighbouring animals. Although the marking procedure is
117 minimally invasive and often elicited no reaction from the pup, we waited at least 15 minutes after
118 marking to ensure that animals returned to a baseline behaviour before recordings were made. Mothers
119 were identified using natural marks (fur colour pattern and scars) or through their association with their
120 marked pup. As males are very active and spend time in the shallow water area at Pelican Point, they
121 were identified with oil-based paint marks made with a roll mounted on a 5-m pole.

122 *Cape Cross* – We did not mark animals as all our individual recordings were made within one
123 or two days at each trip and re-identification over time was not needed (no playback experiments were
124 performed). Seals were only recorded from a limited part of the colony, the tourist walkway and area
125 adjacent to the parking lot. There was no ambiguity about the identity of the emitting individual and we
126 made sure not to sample the same animals (i.e., same location) twice within recording days. All males
127 in the recording area were subadults and thus no territorial and adult bulls could be included in our call
128 collection.

129 For both colonies, age of pups was estimated as follows: very small pups with fresh umbilical
130 cord and/or placenta were categorized as 'less than 24 hours'; small pups with dry and small umbilical
131 cord remains were assigned 'less than 2 weeks'; small pups without umbilical cord remains, recorded at
132 the beginning of December were considered as '1 month' age class. The class '2-4 months' includes only
133 large-size pups showing some signs of moulting and were recorded in February.

134

135 **Recording procedure and signal acquisition**

136 Fur seals' vocalisations were recorded using a Sennheiser ME67 directional shotgun microphone
137 (frequency range: 40 – 20.000 Hz +/- 2.5 dB) at 44.1 kHz sampling frequency connected to a two-
138 channel NAGRA LB or Roland R26 digital audio recorder. While recording, the experimenter described
139 the identity of the animal vocalizing in a lapel microphone connected to the second channel. Distance
140 from focal animals ranged from 0.5 to 6 meters during recording sessions.

141

142 **Calls analysis**

143 The degree of individuality was investigated for five Cape fur seal call types: pup-attraction call (PAC),
144 female-attraction call (FAC), adult male bark (PP only), subadult male bark and female bark for both
145 Pelican Point and Cape Cross colonies (Fig. 1). From the previous literature on pinnipeds, PAC and
146 FAC are affiliative calls produced by mothers and pups respectively in a context of reunion or for short-
147 distance social interactions) (Roux 1986; Phillips and Stirling 2001; Charrier et al. 2002; Tripovich et
148 al. 2008a). Barks are short calls always produced in sequence during agonistic interactions and mating
149 contexts (Roux 1986; Phillips and Stirling 2001; Tripovich et al. 2008a). For PAC and FAC, we selected
150 6 to 10 good-quality calls (i.e., no background noise and no overlap with other vocalising animals) per
151 individual. For barks, we selected between 1 and 10 sequences per individual, and 5 good-quality barks
152 were selected per sequence, resulting in 5 to 50 calls per individual. The selected sequences of barks
153 from adult males were recorded only during interactions with females and territorial defence but not
154 during strong agonistic interactions with rivals or copulation with females. This guaranteed
155 homogeneous arousal states among recorded territorial males.

156 Recordings were converted from stereo to mono and resampled at 22.05 kHz as the highest
157 frequencies of Cape fur seal vocalizations do not exceed 10 kHz. Acoustic analysis was performed using
158 Avisoft SAS Lab Pro (R. Specht, version 5.2.14, Avisoft Bioacoustics, Berlin, Germany) and
159 spectrograms were calculated with a 1024-point fast Fourier transform (FFT), 75% overlap and a
160 Hamming window. To assess the level of individuality occurring in vocalizations, we measured 11 to
161 14 acoustic variables depending on the call type. Total duration of the call (*Dur*; ms), value of the
162 fundamental frequency (*f0*; Hz), frequency value of the 1st, 2nd and 3rd energy peak (*Fmax1*, *Fmax2*,

163 F_{max3} ; Hz), energy quartiles (Q_{25} , Q_{50} , Q_{75} ; Hz), percentage of energy below 500 Hz for adults and
164 below 2000 Hz for pups ($E_{below500}$ or $E_{below2000}$; %) and the frequency bandwidth within which the
165 energy falls within 12 dB of the first peak (B_{dw12} ; Hz) were measured for all call types. The total
166 duration of a call was measured on the oscillogram with a cursor precision of 1 ms and spectral
167 parameters (f_0 , F_{max1} , F_{max2} , F_{max3} , Q_{25} , Q_{50} , Q_{75} , $E_{below500}/E_{below2000}$ and B_{dw12}) were
168 measured from the averaged energy spectrum (Hamming window, frequency range: 0-5000 Hz).

169 In addition to the 10 common variables described above we also measured the slope of the
170 frequency modulation (FM_{slope} ; $\text{Hz}\cdot\text{s}^{-1}$) at the onset of PAC and FAC (Charrier et al. 2002). The
171 FM_{slope} was calculated on the fundamental frequency of the spectrogram (FFT window size: 1024 or
172 512, cursor precision: 30 Hz, 1 ms) by measuring the change in frequency over time from the start of
173 the signal to the first inflection point. If the fundamental frequency was partially filtered by the vocal
174 tract, we measured the slope on upper harmonics and corrected the slope by the appropriate factor (e.g.,
175 slope divided by 2 if measured on the second harmonics, by 3 if third harmonics).

176 As barks are always produced in a sequence, measurements were thus performed on five bark
177 units randomly chosen from each bark sequence. We also measured the inter-bark duration
178 ($InterbarkDur$; duration of the silence between the end of the measured bark and the beginning of the
179 next one) for each of the five randomly selected barks as well as the total duration of the sequence
180 ($DurSeq$; ms) and the bark production rate ($BarkRate$; Hz) for each sequence.

181

182 **Vocal stereotypy in Cape fur seal vocal repertoire**

183 Individual stereotypy in CFS vocalizations was estimated using descriptive and statistical classification
184 methods. In order to optimize the subsequent discrimination among individuals, the individuality
185 encoded in each acoustic variable was assessed for each call type (PAC, FAC, adult male bark, subadult
186 male bark, and female bark) and for each colony – based on two criteria. We firstly used a coefficient
187 of variation (Robisson et al. 1993) and calculated the CV_i (within-individual) and the CV_b (between-
188 individual) according to the formula: $CV = 100 * (1 + 1/4n) * (SD/X_{mean})$ (Sokal and Rohlf 1995). The
189 Potential for Individual Coding (PIC) can thus be calculated with $PIC = CV_b / \text{mean } CV_i$. The PIC value

190 indicates how great the between-individual variation is relative to the within-individual variation and
191 acoustic variables with value > 1 are likely to encode individual identity (Robisson et al. 1993). For
192 barks, since *DurSeq* and *BarkRate* are relative to the sequence and not to individual barks, PIC values
193 for these variables were calculated for individuals with more than 6 sequences of barks and these
194 variables were not included in subsequent classifications. As *FMslope* can be of positive or negative
195 sign (we had both ascending and descending FM pattern), the coefficient of variation was not relevant
196 and thus PIC values were not calculated for this variable. As the data were not normally distributed and
197 did not show homogeneous variances (Shapiro-Wilk and Levene's tests) we tested differences among
198 individuals for each acoustic variable using a series of non-parametric Kruskal-Wallis tests. For FAC,
199 PIC values and Kruskal-Wallis tests were performed on calls from pups of all ages.

200 Individual stereotypy was further investigated using a Random Forest algorithm (RF) performed
201 separately on the five studied call types and from both colonies. RF is a relatively recent and robust
202 method for classification based on averaging multiple decisions trees. It is a useful method for acoustic
203 studies because it does not require assumptions on the distribution of variables and can deal with
204 imbalanced data (Breiman 2001). Analyses were carried out using RStudio Version 1.2.5042 (R
205 Development Core Team (2019) using the package *randomForest* (Liaw and Wiener, 2002). For each
206 call type were interested in how well calls were classified to the individual who produced them.
207 Classification was enhanced by using the most individualized acoustic variables previously identified
208 with PIC values > 1 and significant KW tests. We set the number of trees at 1000 and the number of
209 variables to be selected at each node at 4 because the global error rate stabilised from these values. To
210 equalize the role of each class (i.e. each individual) in the categorization and to avoid the over-
211 representation of the biggest classes, we used the 'Balanced Random Forest' algorithm described by
212 Chen et al. (2004). In this procedure, each tree of the RF is built with the same number of calls per
213 individual (i.e. the smallest number of calls for one individual: 6 for PAC and FAC, and 5 for barks).
214 The Gini index was extracted for each variable and allowed us to classify them according to their degree
215 of contribution to the classification. Classification rates indicated whether the set of acoustic variables
216 can be used to significantly discriminate vocalizations among individuals. For pups' calls, classifications
217 were firstly made on individuals of all ages to assess the overall degree of individuality of FACs within

218 the CFS vocal repertoire. Then, we performed classifications by age-class to monitor the degree of
219 individuality with pups' age. Classification of pups' vocalizations were performed using the balanced
220 classification method with equalized number of individuals ($n=5$ for each iteration). As different
221 parameters may better encode identity in different age classes and maturation effects are interesting to
222 observe, analyses were conducted using all variables measured for FAC in both study sites (all with PIC
223 > 1).

224 Averaged classification rate obviously depends on the degree of individuality in vocalizations
225 but also varies according to the number of individuals included in the sample. With few individuals, it
226 is easier to differentiate vocalizations and obtain a classification rate close to 100%. As the number of
227 individuals increases, the overlap between vocalizations increases and discrimination becomes more
228 difficult. Some individuals are very poorly classified, even not correctly classified at all, and the
229 classification rate decreases drastically. To compare classification rates among samples/studies, we need
230 to consider the probability for a call to be correctly classified by chance, depending on the total number
231 of individuals included in the classification: n . The index of vocal stereotypy (IVS, Charrier 2020) has
232 been proposed as a standardization of classification rates taking into account the number of individuals
233 (n or chance):

$$234 \quad IVS = \frac{CR}{chance} \quad \text{with: } chance = \frac{100}{n}$$

235
236 where CR is the averaged correct classification rate (from RF algorithm here, or DFA/ANN for other
237 studies) and n the number of individuals. IVS were first calculated with the total number of individuals
238 per call type.

239 IVS, which can also be formulated as:

$$240 \quad IVS = \frac{CR \times n}{100}$$

241 This standardisation has however some limitation. Indeed, IVS is highly dependent on the number of
242 individuals, n . This index is thus suitable when comparing groups with similar sample sizes but gets
243 limited if groups show strong differences in sample size (e.g., 10 vs 50). To allow proper comparisons
244 among groups or species, classifications must include samples of similar numbers of individuals to

245 minimise the effect of n . Hence, we secondly used a balanced classification method for each call type
246 (from both colonies) to calculate IVS for multiple n values ranging from 2 to the total number of
247 individuals. For a given value of n , we randomly selected n individuals and performed an RF algorithm
248 ('Balanced Random Forest' algorithm, number of trees: 1000, number of variables at each node: 4). This
249 procedure was repeated 100 times to mix selected individuals and include the entire dataset.
250 Classification rates obtained from each of the 100 iterations were averaged and the resulting value was
251 used to calculate the IVS. This method allowed us to compare IVS from different call types over a wide
252 range of n instead of a single value.

253 In order to compare the degree of individuality of FAC among pup age-classes of different sizes,
254 we used the same balanced classification method. For each age-class, RF algorithm was conducted with
255 all calls (6 to 10 calls per individuals) from 5 randomly selected individuals within the age-class
256 (corresponding to the n of the smallest class). To ensure all individuals of a class are included in the
257 classification, the procedure was repeated 100 times. The resulting averaged classification rates were
258 thus comparable among age-class as they were built with the same sub-sample size.

259

260 **Comparison of vocal individuality between the two study sites**

261 As IVS values have been calculated for each call type and for both colonies over a wide range of n (see
262 above), we can thus compare the level of vocal stereotypy between the two colonies at similar sample
263 sizes.

264

265 **Comparison of vocal individuality among Pinnipeds**

266 The degrees of individuality found for PAC, FAC and adult male barks in Cape fur seal were compared
267 with published values from the same call types from other pinniped species. IVS values comparisons
268 for PAC and FAC were based on the review compiled by Charrier (2020). For male barks, we calculated
269 IVS values from three studies of bark individuality in other Otariid species (Fernández-Juricic et al.
270 1999; Tripovich et al. 2005; Gwilliam et al. 2008). As the number of individuals included in the

271 classification varies among studies, the IVS values we previously calculated for several values of n
272 allowed us to make n -equal comparisons with other studies according to their sample size.

273

274 **Results**

275 After selecting good-quality calls from recordings conducted on our two study sites, we ended up with
276 a dataset of 550 PACs from 66 females, 285 barks from 27 females, 677 FACs from 76 pups and 1820
277 barks from 65 males (47 adults and 18 subadults).

278

279 **Individuality of acoustic variables**

280 The PIC (potential for individuality coding) values for the acoustic variables measured from the five
281 types of calls are listed in Table 1. The majority of PIC values were higher than 1 (except in 5 cases with
282 PIC = 1, Table 1) showing that all acoustic variables have greater inter- than intra-individual variation
283 for multiple types of call and are therefore likely to encode individual identity. This is reinforced by the
284 Kruskal-Wallis tests results (mostly significant, Table 1), showing that the majority of the variables have
285 mean values significantly different among individuals, for all types of calls. At the same time, Kruskal-
286 Wallis tests for *FMslope* of PAC and FAC from PP and CC were all highly significant (maximum p-
287 value: 3.22×10^{-10}) and *FMslope* was therefore added to other predictors. For parameters related to the
288 sequence of barks, *Durseq* and *Barkrate*, PIC values were respectively 1.1 and 2 for Pelican Point
289 subadult males and 1.3 and 1.9 for Pelican Point adult males. Kruskal-Wallis tests were all significant.
290 These variables are therefore also likely to encode individual identity but were not used as predictors as
291 related to the sequence and not to individual barks.

292

293 **Vocal stereotypy in Cape fur seal vocal repertoire**

294 The degree of individuality was investigated in five types of calls using Random Forest classification
295 conducted using only the variables with PIC > 1 and significant Kruskal-Wallis tests (these predictors
296 are highlighted in bold in Table 1). The averaged classification rates obtained for each call type and for
297 each colony ranged between 54 to 91%, and were all higher than chance, resulting in IVS values ranging

298 from 4 to 29 (Table 2). IVS values were quite similar in mothers and pups calls, between 11 and 29.
299 Where they were recorded (PP) adult males barks showed a comparable IVS value (26) to affiliative
300 calls produced by mothers and pups. Barks in sub-adult males and adult females presented lower values
301 of IVS, ranging between 4 and 9 (Table 2).

302 *Dur* and *f0* were among the variables contributing the most to the classification of individuals
303 for all call types (high Gini index values, Supp. 1). For affiliative calls, the three energy quartiles and
304 the frequency modulation had also high values of Gini index. Regarding barks, temporal parameters
305 were also investigated and with *InterbarkDur* was important for classification of adult males, although
306 this seemed to have less influence in subadult or female barks (Supp. 1).

307 The IVS values for each type of call as a function of the number of individuals (*n*) are shown in Fig. 2.
308 As expected, IVS values increased with *n* and followed a power function. Our IVS estimation were
309 extrapolated using a power trend line to visualize IVS variation over the whole range of *n* and to facilitate
310 comparisons. However, the PAC curve for Cape Cross seemed a little over-estimated and may likely be
311 flatter. The number of individuals was too small to properly extrapolate IVS values for subadult male
312 barks from Cape Cross. These results are relatively consistent with IVS in Table 2: PAC, FAC and adult
313 male barks show the highest degrees of individuality while female barks and subadult males from Cape
314 Cross showed lower values. This graphical representation pointed out a possible over-estimation of the
315 degree of individuality in adult male barks (Table 1) because of a large number of males (*n*= 47) in our
316 dataset, and similarly, the IVS values for PAC's at Cape Cross (IVS=10.82) are probably underestimated
317 (*n*= 12).

318

319 **Variation of individuality in pups' calls by age-class**

320 We then investigated how individuality of FACs changed over development for pups at both study sites.
321 For the RF, averaged classification rates for each age-class ranged between 73% and 91%. A high
322 classification rate (91%) was found for pups younger than 24 hours, showing an early degree of
323 individuality in their vocalizations. Where comparisons could be made (pups > 24 hrs), classification
324 rates were generally similar between the two colonies with the exception of a slight offset in
325 classification rates for 1-month age-class from Pelican Point (Fig. 3). However, classification rates did

326 not change significantly with age or within age classes between colonies. At the younger age classes
327 (under 1-month), f_0 and either FM_{slope} or the energy quartiles (Q_{25} , Q_{50}) are the most important
328 parameters in individual classification for FACs. For the older age class (2-4 months), f_0 remains
329 important but now the duration (Dur) is also of relevance.

330

331 **Comparison of vocal individuality level in two study sites**

332 IVS values for each call type as a function of the number of individuals were calculated for our two
333 study sites: Pelican Point and Cape Cross (Fig. 2). We found that, with samples of equal size,
334 vocalizations produced at the larger colony with landmarks (Cape Cross) have a higher degree of
335 individuality compared to Pelican Point for PAC, FAC and female barks.

336

337 **Comparison of vocal individuality level among Pinnipeds**

338 We compared the IVS values obtained at the two study sites using different n values to those obtained
339 with other pinniped species (extracted from Charrier 2020 for FAC and PAC, and measured here for
340 male barks) (Fig. 4). For PAC produced by females, Cape fur seal IVS values were similar or greater
341 than most otariid species (PP being lower to South American sea lion and Steller sea lion and CC only
342 lower to South American sea lion) and greater than all phocids species. The IVS in Cape fur seal FACs
343 differed less between the colonies and were higher than all pinniped species except the South American
344 sea lion. Considering the adult male barks, Cape fur seals showed higher IVS values than the Australian
345 fur seal and sea lion, but lower than South American sea lion.

346

347 **Discussion**

348 **Individual stereotypy in CFS vocalisations**

349 This study investigated the degree of individuality encoded in Cape fur seal vocalizations and assessed
350 the potential role of vocal signals in recognition among conspecifics. Five types of calls from pups,
351 males and females at different ages were taken into consideration. All of the acoustic features included
352 in the analysis (11 to 14 depending on call types) demonstrated individual stereotypy with PIC values

353 >1. Parameters in both temporal and frequency domains varied among individuals and conveyed
354 information about individual identity. PIC values were relatively similar among variables (range: 1-5.1,
355 median: 1.5), meaning that individuality is likely to be supported by a combination of acoustic features
356 rather than a uni-factorial process.

357 We observed a clear dichotomy in the degree of individual stereotypy among call types:
358 affiliative calls (FAC and PAC) and territorial call (barks from adult males) showed high IVS values
359 whereas agonistic calls (barks from females and subadult males) have lower IVS values. This finding is
360 further discussed below.

361 *Affiliative calls* – Otariids species are subject to high selective pressures for mother-offspring
362 recognition: frequent absences of females to forage at sea means females need to regularly localize their
363 pup in high density breeding colonies throughout the long period of pup dependence. Hence, pup- and
364 female-attraction calls, produced during mother-pup reunions, are expected to convey reliable and
365 distinguishable information about the identity of the emitter. Evidence of vocal stereotypy in mother-
366 pup pair vocalizations were shown in all otariids species that have been examined so far (Stirling 1971;
367 Stirling and Warneke 1971; Trillmich 1981; Insley 1992; Fernández-Juricic et al. 1999; Phillips and
368 Stirling 2000; Charrier et al. 2002, 2003; Page et al. 2002; Tripovich et al. 2009, 2006). As expected,
369 we found a high degree of individuality in Cape fur seal affiliative calls (Table 2). Regarding similar
370 IVS values found for PAC and FAC, mother-offspring vocal recognition might be mutual in Cape fur
371 seal, as it has been shown with playback experiments for other otariids species: the Subantarctic fur seal
372 (Charrier et al. 2001b, 2002), the northern fur seal (Insley 2000, 2001) and the Australian sea lion
373 (Charrier et al. 2009; Pitcher et al. 2012). This requires that both mothers and pup have the sensory and
374 cognitive abilities to decode the information contained in their vocalisations. For both PAC and FAC,
375 the fundamental frequency (f_0) and total duration of the call (Dur) were important variables for
376 discriminating individuals (Supp. 1). This is mostly consistent with other studies on mammal species in
377 which fundamental frequency was reported to be a good marker of individuality (pinnipeds: Charrier et
378 al., 2002; Perry & Renouf, 1988b; Phillips & Stirling, 2000; sheep: Sèbe, Duboscq, Aubin, Ligout, &
379 Poindron, 2010; goats: Briefer & McElligott, 2011; Torriani, Vannoni, & McElligott, 2006; dingo:

380 Déaux, Charrier, & Clarke, 2016). In contrast, the duration of the call individual-specific for some
381 species (Insley 1992; Fernández-Juricic et al. 1999; Phillips and Stirling 2000; Charrier et al. 2003;
382 Tripovich et al. 2006, 2009) and not for others (Charrier et al. 2002). Features such as *f0* and *Dur* are
383 source-related acoustic cues (source-filter theory, Taylor & Reby, 2010) and are linked to anatomic
384 features of the emitter such as lung capacity (relative to body size) and vibrations of the vocal folds.
385 This is therefore not surprising that these acoustic variables play a major role in the discrimination
386 among individuals. Filter-related features such as the energy spectrum were also important for the
387 discrimination among individuals, and are known to be used for individual recognition in species
388 including pinnipeds (Jouventin & Aubin 2002, Charrier et al., 2002, 2003; Pitcher, Harcourt, & Charrier,
389 2010; Sèbe et al. 2010, Tripovich, Charrier, Rogers, Canfield, & Arnould, 2008a; Mathevon et al. 2017).

390 We investigated individuality in pups' calls at different ages, and found that the degree of vocal
391 stereotypy was already high within the first 24 hours of life and varied little over development (Fig 3).
392 This clearly shows that individuality in pups' vocalizations is an innate process related to anatomical
393 differences among individuals from a very early age (likely from birth), and thus no vocal learning
394 mechanism is involved: i.e. unlike other marine mammals such as dolphins (Janik and Sayigh 2013),
395 they do not learn individual distinctiveness. Early individual stereotypy in CFS pup calls also indicates
396 that vocal recognition of a pup by its mother might occur within the first week before the mother's first
397 departure to sea. Indeed, Australian sea lion females which are exposed to lower social/environmental
398 constraints on recognition than CFS, can accurately discriminate their pup's calls from others 48 hours
399 after parturition (Pitcher et al. 2010). Such early vocal recognition is likely to occur in CFS but remains
400 to be tested. The degree of individual stereotypy in pup calls is relatively stable throughout the first
401 months of life (Fig. 3). This is consistent with a previous study on Australian fur seals (Tripovich et al.
402 2009) in which DFA classification rates were similar between newborn and 9- to 11-month-old pups.
403 We observed a slight decrease in classification rates for the 1-month age-class from Pelican Point
404 (Fig.3). We hypothesize that at this period the mother's foraging trips at sea begin to get longer
405 (Kirkman, unpublished data) and pups vocalizations might be slightly more variable due to a higher
406 emotional and motivational state (i.e., transition period from short to longer maternal absence) (Briefer
407 2012).

408 *Territorial calls* –Territorial males establish and maintain their territories through aggressive
409 behaviour including through the production of barks. Individual vocal recognition may therefore be
410 highly important for a male to assess the identity of surrounding males. Vocal stereotypy contained in
411 adult male barks is likely to be an advantage to distinguish neighbours from potential challengers
412 (strangers) and thus reduce the number of physical conflicts during the breeding season (Roux and
413 Jouventin 1987; Bee and Gerhardt 2001). Among Otariid species, individuality in male vocalizations
414 has been shown in threat calls (Insley et al. 2003), as well as in barks of three species: South American
415 sea lion (Fernández-Juricic et al. 1999), Australian sea lion (Gwilliam et al. 2008) and Australian fur
416 seal (Tripovich et al. 2005) for which the existence of an individual recognition between males
417 (neighbours-strangers) has been experimentally proven (Tripovich et al. 2008c). In CFS the IVS values
418 found for adult male barks were as high as those found for affiliative calls and demonstrate that adult
419 male barks are individual-specific. We hypothesise that adult male barks convey enough information
420 about identity to enable females to recognize the territorial male of their harem, and for males to
421 discriminate among neighbouring males. Several acoustic features may allow individual vocal
422 discrimination, such as the bark rate, bark sequence duration, as well as both source- and filter-related
423 features.

424 *Agonistic calls* – Subadult males are sexually mature but too young socially to hold a harem.
425 They are found on the edge of the colony and produced barks during agonistic interactions with adult
426 and subadult males, but also when approaching females as potential mates. CFS females also produce
427 barks during agonistic interactions with other conspecifics. Considering the agonistic context in which
428 these barks are produced, we did not expect a high degree of individuality as in territorial males' barks.
429 Such level of individuality (IVS ranging from 4 to 8) could be mostly explained by anatomical
430 differences among individuals (source-filter theory), but the biological function is unlikely an
431 evolutionary driver of vocal individuality. As for other call types, both duration of the call and the
432 fundamental frequency values were the most useful explanatory variables (Supp. 1). The bark rate
433 (*InterbarkDur*) was much less important for subadult and female barks than for adult males showing a
434 less stable calling rate in these two classes of individuals. Keeping a consistent and stable call rate has
435 been shown in the threat calls of Northern elephant seal adults (Casey et al. 2015), with subadult males

436 being more variable but improving with age (Casey et al. 2020). A similar vocal maturity might occur
437 in CFS, with males being able to produce a stable bark rate when getting socially mature.

438 This study is unusual in comparing the individuality level of a species at the vocal repertoire
439 scale (Fernández-Juricic et al. 1999) as previous studies mainly focus on one or two call types (especially
440 pup- and female-attraction calls). We showed that, in accordance with other taxa (Mitani et al. 1996;
441 Charrier et al. 2001a; Mathevon et al. 2003; Leliveld et al. 2011; Déaux et al. 2016), the individuality
442 level in Cape fur seal vocalizations is linked to the social role of the individual (territorial vs. non-
443 territorial, female vs. male) and the biological function of the call (affiliative, territorial, agonistic), with
444 the most individualized being affiliative and territorial.

445

446 **Comparison of Vocal stereotypy between study sites**

447 The second aim of this study was to compare the degrees of vocal individuality between breeding
448 colonies. We hypothesized a greater degree of individuality in calls from Pelican Point individuals
449 (especially affiliative calls) because of the homogeneity of the site and the lack of topographical
450 landmarks facilitating localisation, especially for mother-pup reunions. In contrast, PAC, FAC and
451 female barks from Cape Cross presented higher IVS values than those from Pelican Point (Fig. 4). As
452 our recording procedures and acoustic analyses were exactly the same between the two sites and there
453 was no difference in sample size due to our balanced classification method, we can be confident that
454 these observed differences are not related to the methodology. In social species, group size can influence
455 the individual distinctiveness of acoustic signals (in rodents: Pollard & Blumstein, 2011; in bats:
456 Wilkinson, 2003). We thus suggest that both seal numbers and colony density (much higher at CC than
457 PP) and ecological/physical constraints (more wave noise at CC than at PP, different wind exposure)
458 might explain such differences. Through an adaptive process, these pressures could act as drivers for
459 different levels of individuality as suggested for two populations of South American sea lions (Trimble
460 and Charrier 2011).

461

462 **Comparison of vocal stereotypy across Pinnipeds**

463 Our last goal was to compare vocal stereotypy in call types among different pinniped species for which
464 published data are available. As the index of vocal stereotypy is only directly comparable between
465 studies with similar sample sizes, we presented IVS values for 19 studies of 17 pinniped species as a
466 function of n (the number of individuals included in the classification). As predicted by their ecological
467 constraints CFS clearly show higher levels of individuality at any given sample size than any other
468 pinniped species - with the exception of the South American sea lion (SASL). As this study on SASL
469 (Fernández-Juricic et al. 1999) is based on a very low number of calls per individual (3 calls/ind),
470 classification rates might thus be over-estimated and CFS might be the species with the most
471 individualized vocalizations. The existence of a relationship between vocal stereotypy and selective
472 pressures for individual recognition has been firstly demonstrated in bird species (Aubin & Jouventin
473 2002, Mathevon et al. 2003). Among penguins, species with the highest ecological constraints for
474 individual recognition (high colony density, absence of nests, high background noise) show a higher
475 vocal stereotypy in their vocalizations compared to species facing fewer constraints (low colony density,
476 presence of nest) (Aubin & Jouventin, 2002). The present study provides additional evidence of the
477 existence of a similar pattern between vocal individuality and complexity of social structure in
478 Pinnipeds, recently mentioned by Charrier (Charrier 2020). Species with the highest degrees of vocal
479 stereotypy showed similar selective pressure for individual recognition: living in moderate to extremely
480 dense colonies and showing high level of polygyny (Cape fur seal, South American sea lion,
481 Subantarctic fur seal or Steller sea lion) (Riedman 1990). All these examples in both birds and mammal
482 species clearly show the importance of social and environmental constraints on the shape of acoustic
483 signals but also on the information-content of vocalisations.

484

485 The presence of vocal stereotypy in vocalizations is not sufficient to argue the occurrence of
486 individual vocal recognition. Further investigations and experimental playback studies are thus needed
487 to confirm individual vocal recognition between mothers and pups, among territorial males, and between
488 territorial males and their harem females. The ecological constraints met by this species can influence
489 the ontogeny of vocal recognition in mother-pup pairs, as well as the complexity of their individual
490 signature.

References

- Aubin T, Jouventin P (1998) Cocktail-party effect in king penguin colonies. *Proc R Soc B Biol Sci* 265:1665–1673. <https://doi.org/10.1098/rspb.1998.0486>
- Aubin T, Jouventin P (2002) How to vocally identify kin in a crowd: The penguin model. *Adv Study Behav* 31:243–277. [https://doi.org/10.1016/s0065-3454\(02\)80010-9](https://doi.org/10.1016/s0065-3454(02)80010-9)
- Bee MA, Gerhardt HC (2001) Neighbour-stranger discrimination by territorial male bullfrogs (*Rana catesbeiana*): I. Acoustic basis. *Anim Behav* 62:1129–1140. <https://doi.org/10.1006/anbe.2001.1851>
- Bradbury JW, Vehrencamp SL (2011) *Principles of Animal Communication*, 2nd edn Sunderland., MA: Sinaue
- Breiman L (2001) Random forests. *Mach Learn* 45:5–32
- Briefer E, McElligott AG (2011) Indicators of age, body size and sex in goat kid calls revealed using the source-filter theory. *Appl Anim Behav Sci* 133:175–185. <https://doi.org/10.1016/j.applanim.2011.05.012>
- Briefer EF (2012) Vocal expression of emotions in mammals: Mechanisms of production and evidence. *J Zool* 288:1–20. <https://doi.org/10.1111/j.1469-7998.2012.00920.x>
- Carter GG, Logsdon R, Arnold BD, et al (2012) Adult vampire bats produce contact calls when isolated: Acoustic variation by species, population, colony, and individual. *PLoS One* 7:. <https://doi.org/10.1371/journal.pone.0038791>
- Casey C, Charrier I, Mathevon N, et al (2020) The genesis of giants: Behavioural ontogeny of male northern elephant seals. *Anim Behaviour* 166:247–259. <https://doi.org/10.1016/j.anbehav.2020.06.014>
- Casey C, Charrier I, Mathevon N, Reichmuth C (2015) Rival assessment among northern elephant seals: Evidence of associative learning during male–male contests. *R Soc Open Sci* 2:. <https://doi.org/10.1098/rsos.150228>
- Charrier I (2020) Mother–Offspring Vocal Recognition and Social System in Pinnipeds. In: Aubin T, Mathevon N (eds) *Coding Strategies in Vertebrate Acoustic Communication*, Springer. pp 231–246
- Charrier I, Jouventin P, Mathevon N, Aubin T (2001a) Individual identity coding depends on call type in the South Polar skua *Catharacta maccormicki*. *Polar Biol* 24:378–382. <https://doi.org/10.1007/s003000100231>
- Charrier I, Mathevon N, Jouventin P (2003) Individuality in the voice of fur seal females: an analysis study of the pup attraction call in *Arctocephalus tropicalis*. *Mar Mammal Sci* 19:161–172
- Charrier I, Mathevon N, Jouventin P (2002) How does a fur seal mother recognize the voice of her pup? An experimental study of *Arctocephalus tropicalis*. *J Exp Biol* 205:603–612
- Charrier I, Mathevon N, Jouventin P (2001b) Mother’s voice recognition by seal pups. *Nature* 412(6850):873–873
- Charrier I, Mathevon N, Jouventin P, Aubin T (2001c) Acoustic communication in a black-headed gull colony: How do chicks identify their parents? *Ethology* 107:961–974. <https://doi.org/10.1046/j.1439-0310.2001.00748.x>
- Charrier I, Pitcher BJ, Harcourt RG (2009) Vocal recognition of mothers by Australian sea lion pups: individual signature and environmental constraints. *Anim Behav* 78:1127–1134. <https://doi.org/10.1016/j.anbehav.2009.07.032>
- Chen C, Liaw A, Breiman L (2004) Using Random Forest to Learn Imbalanced Data | Department of Statistics. Univ California, Berkeley 110:1–12
- David JHM, Rand RW, Kooyman GL (1986) Attendance Behavior of South African Fur Seals. In: *Fur seals: maternal strategies on land and at sea*. pp 126–141
- De Villiers DJ, Roux JP (1992) Mortality of newborn pups of the South African fur seal *Arctocephalus pusillus*

- pusillus in Namibia. *South African J Mar Sci* 12:881–889. <https://doi.org/10.2989/02577619209504749>
- Déaux ÉC, Charrier I, Clarke JA (2016) The bark, the howl and the bark-howl: Identity cues in dingoes' multicomponent calls. *Behav Processes* 129:94–100. <https://doi.org/10.1016/j.beproc.2016.06.012>
- Fernández-Juricic E, Campagna C, Enriquez V, Ortiz CL (1999) Vocal communication and individual variation in breeding South American Sea Lions. *Behaviour* 136:495–517. <https://doi.org/10.1163/156853999501441>
- Fisher JB (1954) Evolution and bird sociality. In: Huxley J, Hardy AC, Ford EB (eds) *Evolution as a Process*. pp 71–83
- Freeberg TM, Dunbar RIM, Ord TJ (2012) Social complexity as a proximate and ultimate factor in communicative complexity. *Philos Trans R Soc B* 367:1785–1801. <https://doi.org/10.1098/rstb.2011.0213>
- Gamel C, Davis RW, David JHM, et al (2005) Reproductive energetics and female attendance patterns of Cape Fur Seals (*Arctocephalus pusillus pusillus*) during early lactation. *Am Midl Nat* 153:152–170. [https://doi.org/10.1674/0003-0031\(2005\)153\[0152:REAFAP\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2005)153[0152:REAFAP]2.0.CO;2)
- Gwilliam J, Charrier I, Harcourt RG (2008) Vocal identity and species recognition in male Australian sea lions, *Neophoca cinerea*. *J Exp Biol* 211:2288–2295. <https://doi.org/10.1242/jeb.013185>
- Halliday TR, Slater PJB (1983) *Animal behaviour*, vol. 2. Communication
- Insley SJ (1992) Mother-offspring separation and acoustic stereotypy: a comparison of call morphology in two species of pinnipeds. *Behaviour* 120:103–122. <https://doi.org/10.1017/CBO9781107415324.004>
- Insley SJ (2000) Long-term vocal recognition in the northern fur seal. *Nature* 406:404–405. <https://doi.org/10.1038/35019064>
- Insley SJ (2001) Mother-offspring vocal recognition in northern fur seals is mutual but asymmetrical. *Anim Behav* 61:129–137. <https://doi.org/10.1006/anbe.2000.1569>
- Insley SJ, Phillips A V., Charrier I (2003) A review of social recognition in pinnipeds. *Aquat Mamm* 29:181–201. <https://doi.org/10.1578/016754203101024149>
- Janik VM, Sayigh LS (2013) Communication in bottlenose dolphins: 50 years of signature whistle research. *J Comp Physiol A Neuroethol Sensory, Neural, Behav Physiol* 199:479–489. <https://doi.org/10.1007/s00359-013-0817-7>
- Jouventin, P., & Aubin, T. (2002). Acoustic systems are adapted to breeding ecologies: Individual recognition in nesting penguins. *Animal Behaviour*, 64(5), 747–757. <https://doi.org/10.1006/anbe.2002.4002>
- Kirkman S (2010) The Cape fur seal: monitoring and management in the Benguela current ecosystem
- Knörnschild M, Fernandez AA, Nagy M (2020) Vocal information and the navigation of social decisions in bats : Is social complexity linked to vocal complexity? *Funct Ecol* 322–331. <https://doi.org/10.1111/1365-2435.13407>
- Leliveld LMC, Scheumann M, Zimmermann E (2011) Acoustic correlates of individuality in the vocal repertoire of a nocturnal primate (*Microcebus murinus*) . *J Acoust Soc Am* 129:2278–2288. <https://doi.org/10.1121/1.3559680>
- Lengagne T, Jouventin P, Aubin T (1999) Finding one's mate in a king penguin colony: Efficiency of acoustic communication. *Behaviour* 136:833–846. <https://doi.org/10.1163/156853999501595>
- Liaw A, Wiener M (2002) Classification and Regression by randomForest. *R News* 2:18–22
- Mathevon N (1997) Individuality of contact calls in the Greater Flamingo *Phoenicopterus ruber* and the problem of background noise in a colony. *Ibis (Lond 1859)* 139:513–517.

919X.1997.tb04667.x

- Mathevon N, Casey C, Reichmuth C, Charrier I (2017) Northern Elephant Seals Memorize the Rhythm and Timbre of Their Rivals' Voices. *Curr Biol* 27:2352-2356.e2. <https://doi.org/10.1016/j.cub.2017.06.035>
- Mathevon N, Charrier I, Jouventin P (2003) Potential for individual recognition in acoustic signals: A comparative study of two gulls with different nesting patterns. *Comptes Rendus - Biol* 326:329-337. [https://doi.org/10.1016/S1631-0691\(03\)00072-6](https://doi.org/10.1016/S1631-0691(03)00072-6)
- Mitani JC, Gros-Louis J, Macedonia JM (1996) Selection for acoustic individuality within the vocal repertoire of wild chimpanzees. *Int J Primatol* 17:569-583. <https://doi.org/10.1007/BF02735192>
- Page B, Goldsworthy SD, Hindell MA (2002) Individual vocal traits of mother and pup fur seals. *Bioacoustics* 13:121-143. <https://doi.org/10.1080/09524622.2002.9753491>
- Peckre L, Kappeler PM, Fichtel C (2019) Clarifying and expanding the social complexity hypothesis for communicative complexity. *Behav Ecol Sociobiol* 73:. <https://doi.org/10.1007/s00265-018-2605-4>
- Perry EA, Renouf D (1988) Further studies of the role of harbour seal (*Phoca vitulina*) pup vocalizations in preventing separation of mother-pup pairs. *Can J Zool* 66:934-938. <https://doi.org/10.1139/z88-138>
- Phillips A V., Stirling I (2001) Vocal repertoire of South American fur seals, *Arctocephalus australis*: Structure, function, and context. *Can J Zool* 79:420-437. <https://doi.org/10.1139/cjz-79-3-420>
- Phillips A V., Stirling I (2000) Vocal individuality in mother and pup South American Fur Seals, *Arctocephalus Australis*. *Mar Mammal Sci* 16:592-616. <https://doi.org/10.1111/j.1748-7692.2000.tb00954.x>
- Pitcher BJ, Harcourt RG, Charrier I (2012) Individual identity encoding and environmental constraints in vocal recognition of pups by Australian sea lion mothers. *Anim Behav* 83:681-690. <https://doi.org/10.1016/j.anbehav.2011.12.012>
- Pitcher BJ, Harcourt RG, Charrier I (2010) Rapid onset of maternal vocal recognition in a colonially breeding mammal, the Australian sea lion. *PLoS One* 5:. <https://doi.org/10.1371/journal.pone.0012195>
- Pollard KA, Blumstein DT (2011) Social group size predicts the evolution of individuality. *Curr Biol* 21:413-417. <https://doi.org/10.1016/j.cub.2011.01.051>
- Rand RW (1967) The Cape fur seal *Arctocephalus pusillus pusillus* 3. General behaviour on land and at sea. *Sea Fish Inst Investgl Rep* 1-32
- Riedman M (1990) The pinnipeds: seals, sea lions, and walruses, (Vol. 12). Univ of California Press
- Robisson P, Aubin T, Bremond J-C (1993) Individuality in the voice of the Emperor Penguin *Aptenodytes forsteri*: Adaptation to a noisy environment. *Ethology* 94:279-290
- Roux J-P (1986) Sociobiologie de l'Otarie à fourrure d'Amsterdam, *Arctocephalus tropicalis*. Université de Montpellier, Montpellier, France
- Roux JP, Jouventin P (1987) Behavioral Cues to Individual Recognition in the Subantarctic Fur Seal , *Arctocephalus tropicalis* (NOAA Tech. Rep. NMFS)
- Sèbe F, Duboscq J, Aubin T, et al (2010) Early vocal recognition of mother by lambs: contribution of low- and high-frequency vocalizations. *Anim Behav* 79:1055-1066. <https://doi.org/10.1016/j.anbehav.2010.01.021>
- Sherman PW, Reeve H, Pfennig D (1997) Recognition systems. In: Krebs JR, Davies NB (eds) *Behavioural Ecology: An Evolutionary Approach*, Oxford: Bl. pp 69-96
- Sokal RR, Rohlf FJ (1995) *Biometry. The principles and practice of statistics in biological research*. 3rd ed, W.H. Freeman

- Stirling I (1971) Studies on the behaviour of the South Australian fur seal, *Arctocephalus forsteri* (Lesson) I. *Aust J Zool* 19:243–66
- Stirling I, Warneke RM (1971) Implications of a comparison of the airborne vocalizations and some aspects of the behaviour of the two Australian fur seals, *Arctocephalus* spp., on the evolution and present taxonomy of the genus. *Aust J Zool* 19:227–241. <https://doi.org/10.1071/ZO9710227>
- Taylor AM, Reby D (2010) The contribution of source-filter theory to mammal vocal communication research. *J Zool* 280:221–236. <https://doi.org/10.1111/j.1469-7998.2009.00661.x>
- Torriani MVG, Vannoni E, McElligott AG (2006) Mother-young recognition in an ungulate hider species: A unidirectional process. *Am Nat* 168:412–420. <https://doi.org/10.1086/506971>
- Trillmich F (1981) Mutual Mother-Pup Recognition in Galápagos Fur Seals and Sea Lions: Cues Used and Functional Significance. *Behaviour* 78:21–42
- Trimble M, Charrier I (2011) Individuality in South American sea lion (*Otaria flavescens*) mother-pup vocalizations: Implications of ecological constraints and geographical variations? *Mamm Biol* 76:208–216. <https://doi.org/10.1016/j.mambio.2010.10.009>
- Tripovich JS, Canfield R, Rogers TL, Arnould JPY (2009) Individual variation of the female attraction call produced by Australian fur seal pups throughout the maternal dependence period. *Bioacoustics* 18:259–276. <https://doi.org/10.1080/09524622.2009.9753605>
- Tripovich JS, Canfield R, Rogers TL, Arnould JPY (2008a) Characterization of Australian fur seal vocalizations during the breeding season. *Mar Mammal Sci* 24:913–928. <https://doi.org/10.1111/j.1748-7692.2008.00229.x>
- Tripovich JS, Charrier I, Rogers TL, et al (2008b) Acoustic features involved in the neighbour-stranger vocal recognition process in male Australian fur seals. *Behav Processes* 79:74–80. <https://doi.org/10.1016/j.beproc.2008.04.007>
- Tripovich JS, Charrier I, Rogers TL, et al (2008c) Who goes there? Differential responses to neighbor and stranger vocalizations in male Australian fur seals. *Mar Mammal Sci* 24:941–948. <https://doi.org/10.1111/j.1748-7692.2008.00222.x>
- Tripovich JS, Rogers TL, Arnould JPY (2005) Species-specific characteristics and individual variation of the bark call produced by male Australian fur seals, *Arctocephalus pusillus doriferus*. *Bioacoustics* 15:79–96. <https://doi.org/10.1080/09524622.2005.9753539>
- Tripovich JS, Rogers TL, Canfield R, Arnould JPY (2006) Individual variation in the pup attraction call produced by female Australian fur seals during early lactation. *J Acoust Soc Am* 120:502–509. <https://doi.org/10.1121/1.2202864>
- Ward A, Webster M (2016) *Sociality: The Behaviour of Group-Living Animals*
- Wickens P, York AE (1997) Comparative population dynamics of fur seals. *Mar Mammal Sci* 13:241–292. <https://doi.org/10.1111/j.1748-7692.1997.tb00631.x>
- Wilkinson GS (2003) Social and vocal complexity in bats. In: De Waal FBM, Tyack PL (eds) *Animal Social Complexity*, Cambridge: pp 322–341
- R Development Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>

Tables

Table 1 PIC values calculated on acoustic variables for each call type

The variables with PIC values > 1 and significant Kruskal-Wallis test were selected as predictors for Random Forest classification and are identified in bold. Kruskal-Wallis tests were all significant except in cases marked with (NS).

		n	<i>Dur</i>	<i>f0</i>	<i>Fmax1</i>	<i>Fmax2</i>	<i>Fmax3</i>	<i>Q25</i>	<i>Q50</i>	<i>Q75</i>	<i>Ebelow500</i> <i>Ebelow2000</i>	<i>Bdw12</i>	<i>InterbarkDur</i>
PAC ($N_{\text{calls}} = 550$)	CC	12	2.2	5.1	1.6	1.1	1 (NS)	1.8	1.5	1.6	1.9	1.2	
	PP	54	1.7	3.4	1.5	1.2	1.3	2	2.1	2	1.8	1.6	
FAC ($N_{\text{calls}} = 677$)	CC	30	1.9	3.2	1.6	1.3	1.3	1.8	2	1.9	2.2	1.4	
	PP	46	1.8	3.4	1.3	1.4	1.6	1.5	1.6	1.4	1.4	1.3	
Adult male bark ($N_{\text{calls}} = 1330$)	PP	47	2.2	2.1	1.5	1.4	1.1	1.6	1.5	1.4	1.6	1.3	1.7
Subadult male bark ($N_{\text{calls}} = 490$)	CC	7	1.4	1.8	1 (NS)	1	1.1 (NS)	1.1 (NS)	1.1 (NS)	1.1	1.2	1.2	1.1
	PP	11	1.7	1.9	1.2	1.12	1.1	1.4	1.7	1.5	1.5	1.3	1.4
Female bark ($N_{\text{calls}} = 285$)	CC	11	1.4	1.8	1.5	1.2	1	1.8	2	2.3	1.6	1.4	1.5
	PP	16	1.5	1.9	1.3	1	1.2	1.4	1.7	2.3	1.4	1.2	1.2

Table 2 Index of vocal stereotypy calculated for each type of Cape fur seal vocalizations and for each studied colony

IVS is the ratio between the classification rate (CR) and the chance (100/n), with n being the number of individuals.

	n	Classif. rate range (%)	Averaged classif. rate (%)	IVS
Pup-attraction call (PAC)				
Cape Cross	12	80 – 100	90.74	10.88
Pelican Point	54	0 - 100	53.62	28.95
Female-attraction call (FAC)				
Cape Cross	30	37.5 – 100	69.2	20.76
Pelican Point	46	0 - 100	55.31	25.44
Adult male bark				
Pelican Point	47	0 - 100	54.96	25.83
Subadult male bark				
Cape Cross	7	44.45 – 100	58.24	4.08
Pelican Point	11	36.92 – 100	74.06	8.15
Female bark				
Cape Cross	11	46.67 – 100	65.19	7.17
Pelican Point	16	0 – 100	57.33	9.17

Figure captions

Fig. 1 Spectrograms of the five Cape fur seal call types investigated in this study

a: PACs from three different females, b: PACs from one female (M58), c: FAC from three pups at three different age-classes: < 2 weeks, 1 month and 2-4 months, d: FACs from one < 2 weeks-old pup (P40), e: female barks, f: adult male barks, g: subadult male barks.

Fig. 2 Variation of the IVS values as a function of the number of individuals sampled (n) for each call type and each study colony

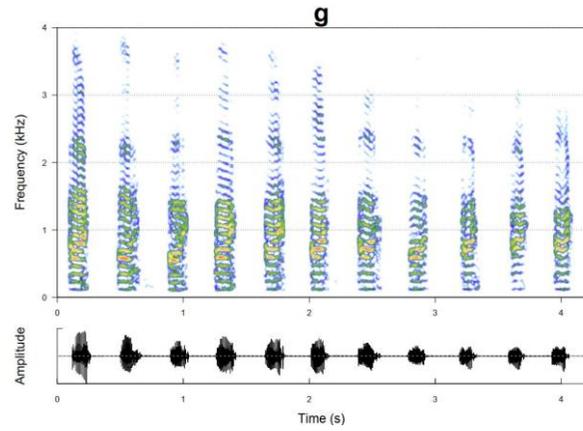
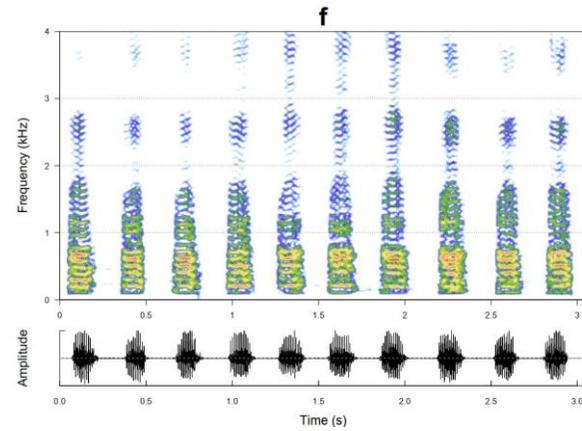
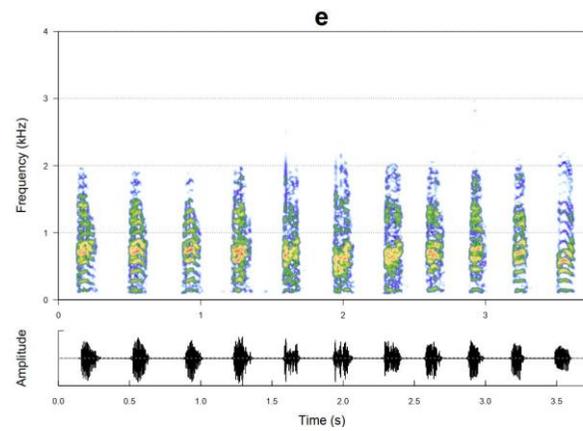
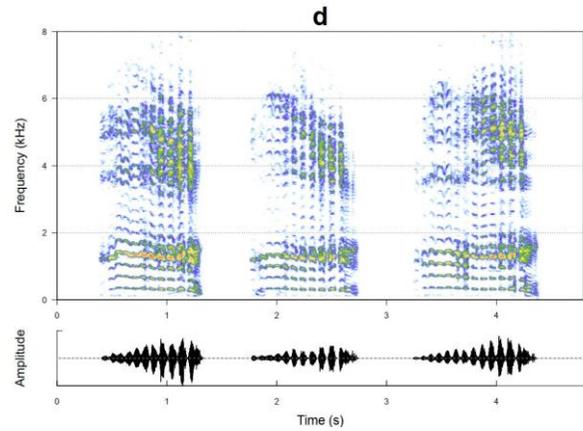
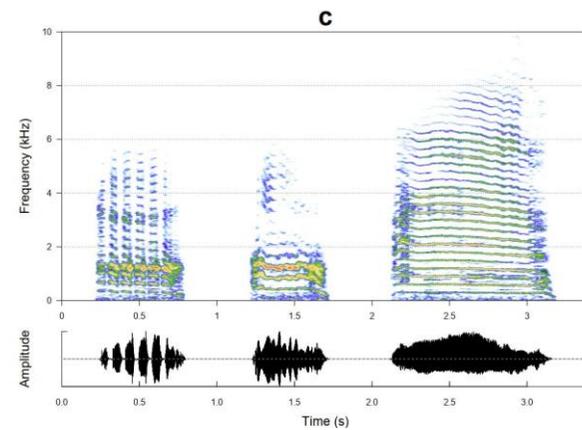
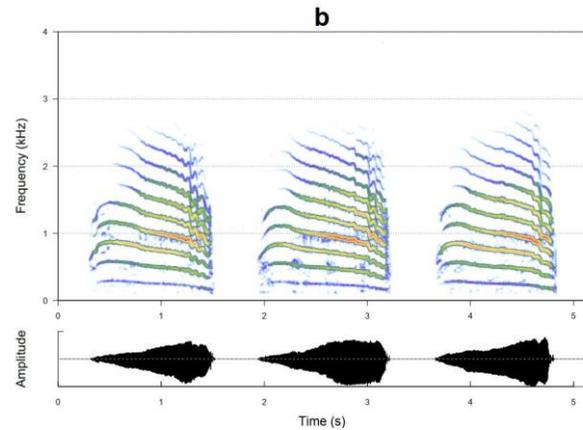
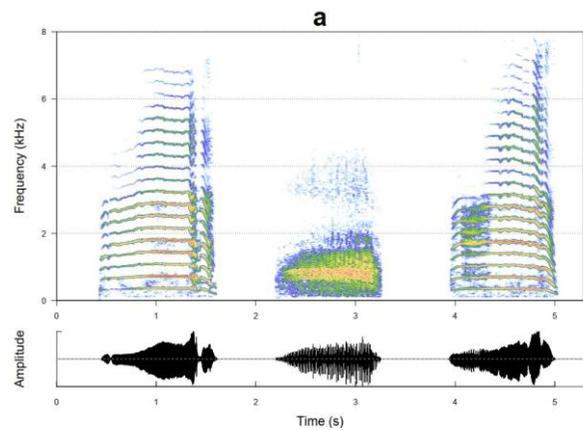
Dots and triangles represent the estimates made on datasets from Pelican Point and Cape Cross respectively. Dotted lines are power trend lines calculated when n values were sufficient.

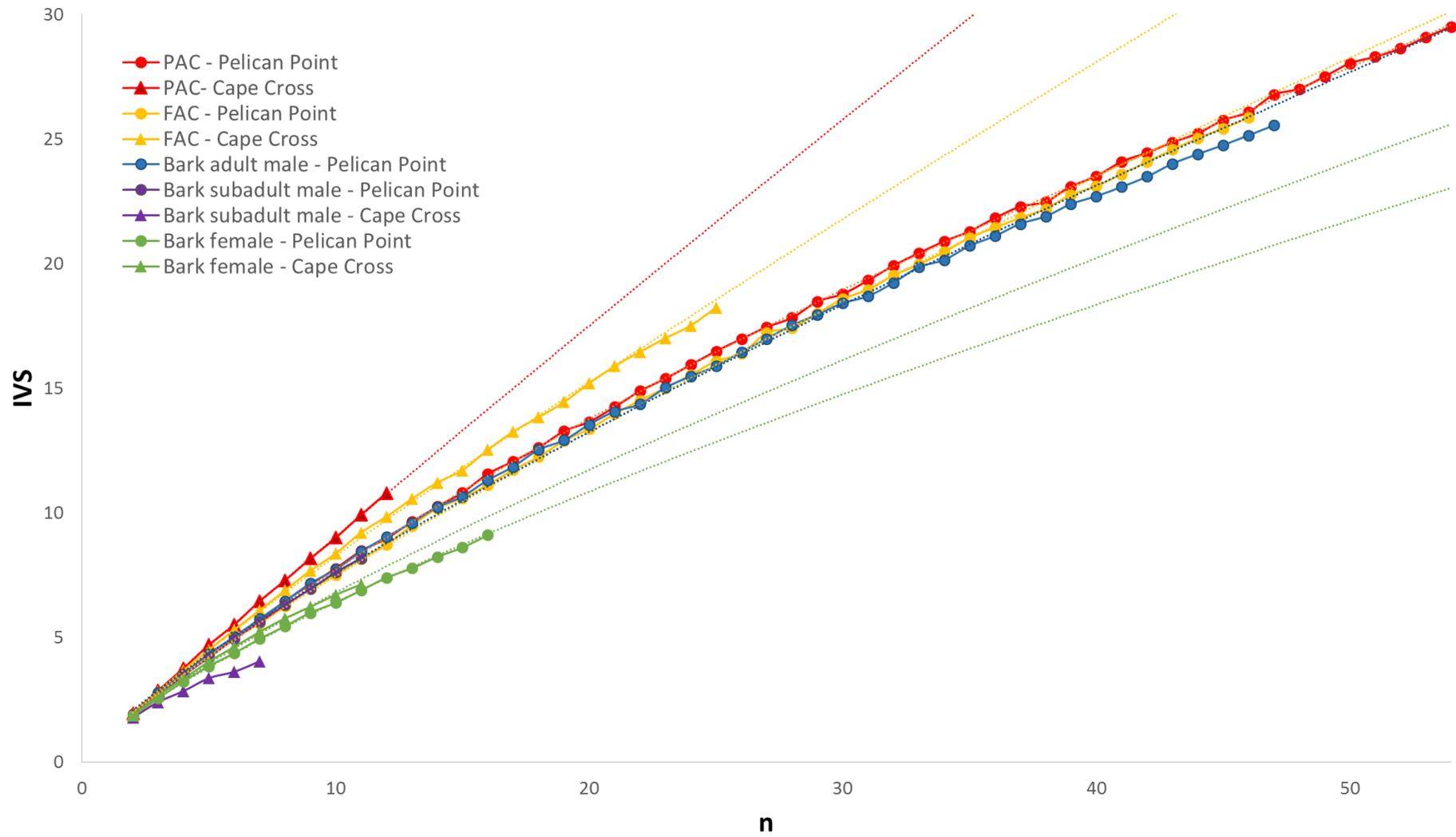
Fig. 3 Classification rates from Random Forest in female-attraction calls (FACs) according to pups' age-classes with a balanced classification method

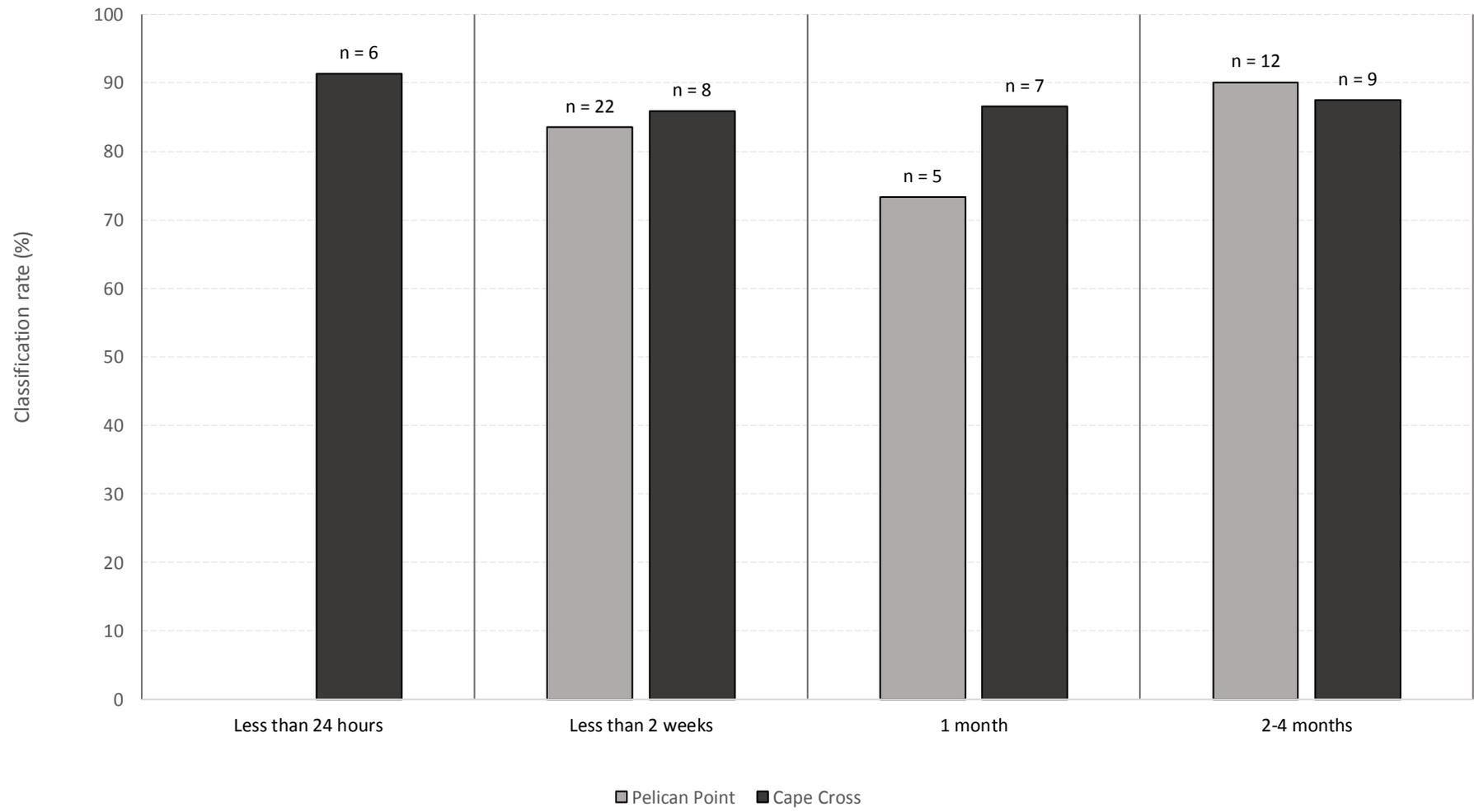
We randomly selected 5 individuals (i.e., *lowest sample size*) and performed a RF algorithm (number of trees: 1000 and number of variables at each node: 4). This procedure was repeated 100 times to mix selected individuals and include all the dataset.

Fig. 4 IVS comparisons among pinnipeds species for three call types: Pup-attraction call (a), Female-attraction call (b) and Adult male bark (c)

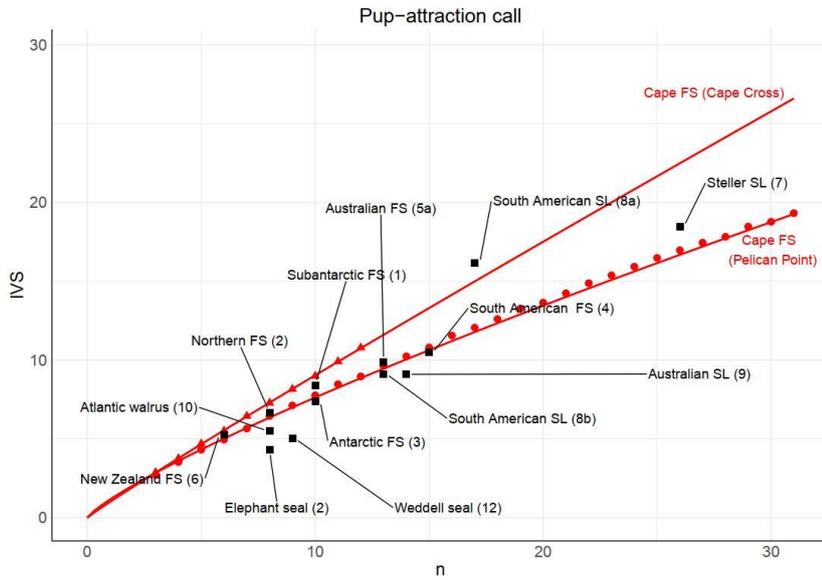
PAC and FAC IVS values were extracted from Charrier et al. (2020). Values for male barks were calculated for this study from cited publications. References: 1: (Page, Goldsworthy, & Hindell, 2002), 2: (Insley, 1992), 3: (Page et al., 2002), 4: (Phillips & Stirling, 2000), 5a: (Tripovich, Rogers, Canfield, & Arnould, 2006), 5b: (Tripovich, Canfield, Rogers, & Arnould, 2009), 6: (Dowell, 2005; Page et al., 2002), 7: (Campbell, Gisiner, Helweg, & Milette, 2002), 8a: (Fernández-Juricic, Campagna, Enriquez, & Ortiz, 1999), 8b: (Trimble & Charrier, 2011), 9: (Charrier & Harcourt, 2006), 10: (Charrier, Aubin, & Mathevon, 2010), 11: (McCulloch, Pomeroy, & Slater, 1999), 12: (K. T. Collins et al., 2005; Kym T. Collins, Terhune, Rogers, Wheatley, & Harcourt, 2006), 13: (Van Opzeeland, Corkeron, Risch, Stenson, & Van Parijs, 2009), 14: (Sauvé, Beauplet, Hammill, & Charrier, 2015), 15: (Job, Boness, & Francis, 1995), 16: (Gwilliam, Charrier, & Harcourt, 2008), 17: (Tripovich, Rogers, & Arnould, 2005).



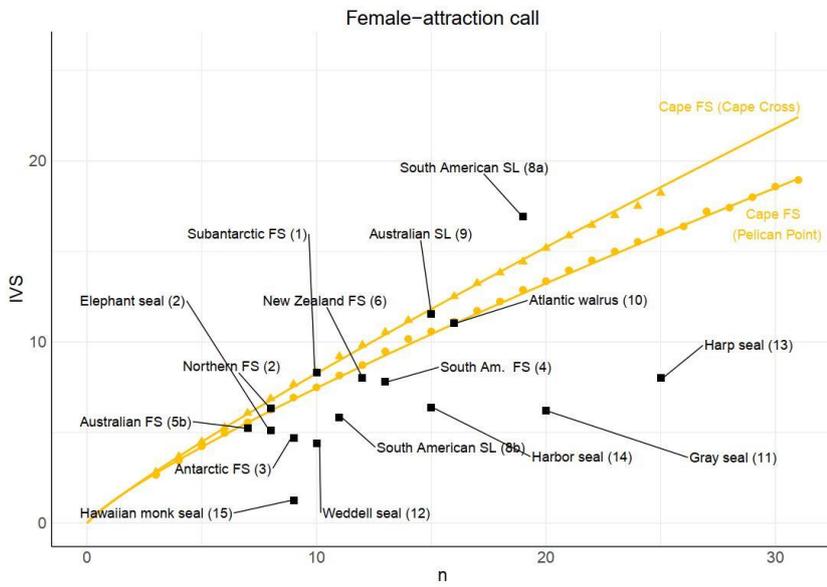




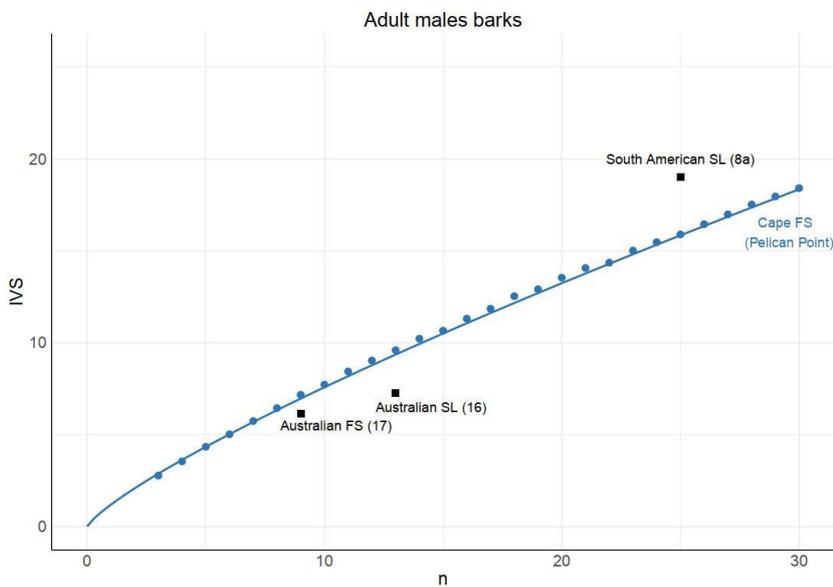
a



b



c





Click here to access/download
Supplementary Material
Supplementary Material.docx

