



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

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

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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

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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.

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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

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

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

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

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

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

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

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

Methods

Study area

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

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

Animal identification

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

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

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

Recording procedure and signal acquisition

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

Calls analysis

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

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

Fmax3; Hz), energy quartiles (*Q25*, *Q50*, *Q75*; Hz), percentage of energy below 500 Hz for adults and below 2000 Hz for pups (*Ebelow500* or *Ebelow2000*; %) and the frequency bandwidth within which the energy falls within 12 dB of the first peak (*Bdw12*; Hz) were measured for all call types. The total duration of a call was measured on the oscillogram with a cursor precision of 1 ms and spectral parameters (*f0*, *Fmax1*, *Fmax2*, *Fmax3*, *Q25*, *Q50*, *Q75*, *Ebelow500/Ebelow2000* and *Bdw12*) were measured from the averaged energy spectrum (Hamming window, frequency range: 0-5000 Hz).

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

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

Vocal stereotypy in Cape fur seal vocal repertoire

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

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

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

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

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

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

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

IVS, which can also be formulated as:

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

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

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

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

Comparison of vocal individuality between the two study sites

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

Comparison of vocal individuality among Pinnipeds

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

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

Results

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

Individuality of acoustic variables

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

Vocal stereotypy in Cape fur seal vocal repertoire

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

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

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

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

Variation of individuality in pups' calls by age-class

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

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

Comparison of vocal individuality level in two study sites

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

Comparison of vocal individuality level among Pinnipeds

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

Discussion

Individual stereotypy in CFS vocalisations

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

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

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

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

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

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

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

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

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

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

Comparison of Vocal stereotypy between study sites

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

Comparison of vocal stereotypy across Pinnipeds

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

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

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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

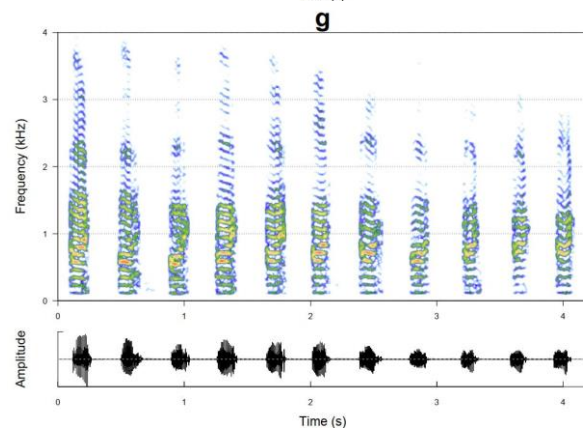
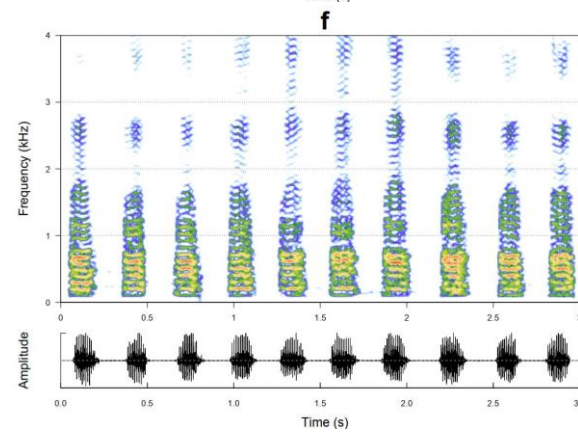
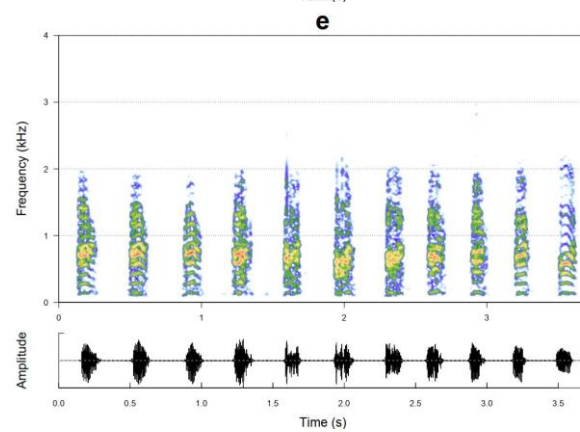
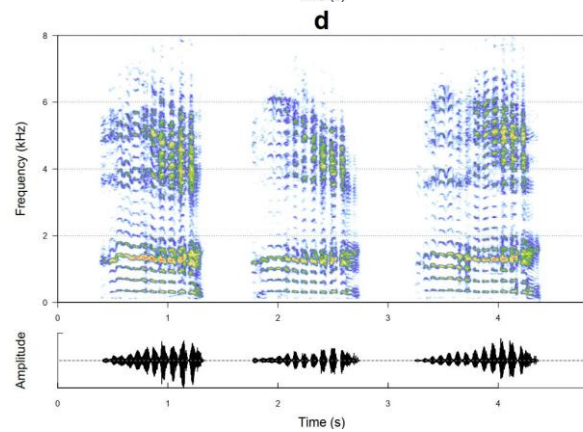
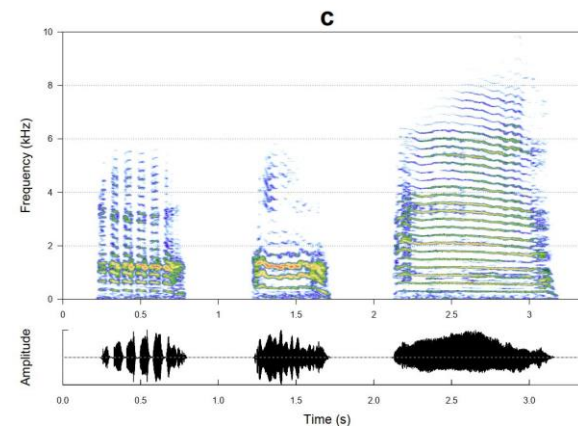
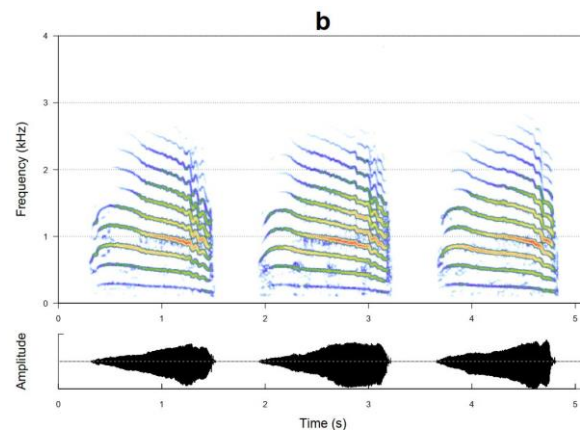
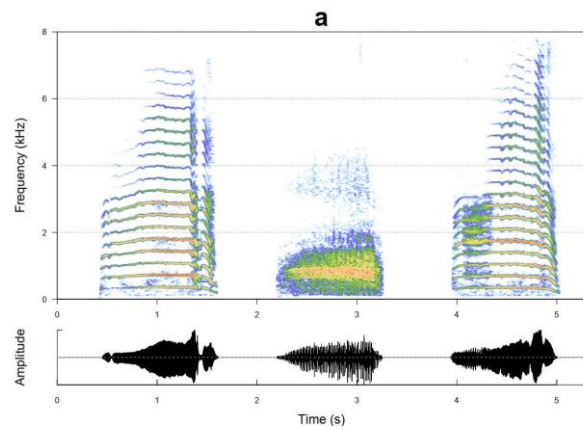
Dots and triangles represent the estimates made on datasets from Pelican Point and Cape Cross respectively. Dotted lines are power trend lines calculated when n values were sufficient.

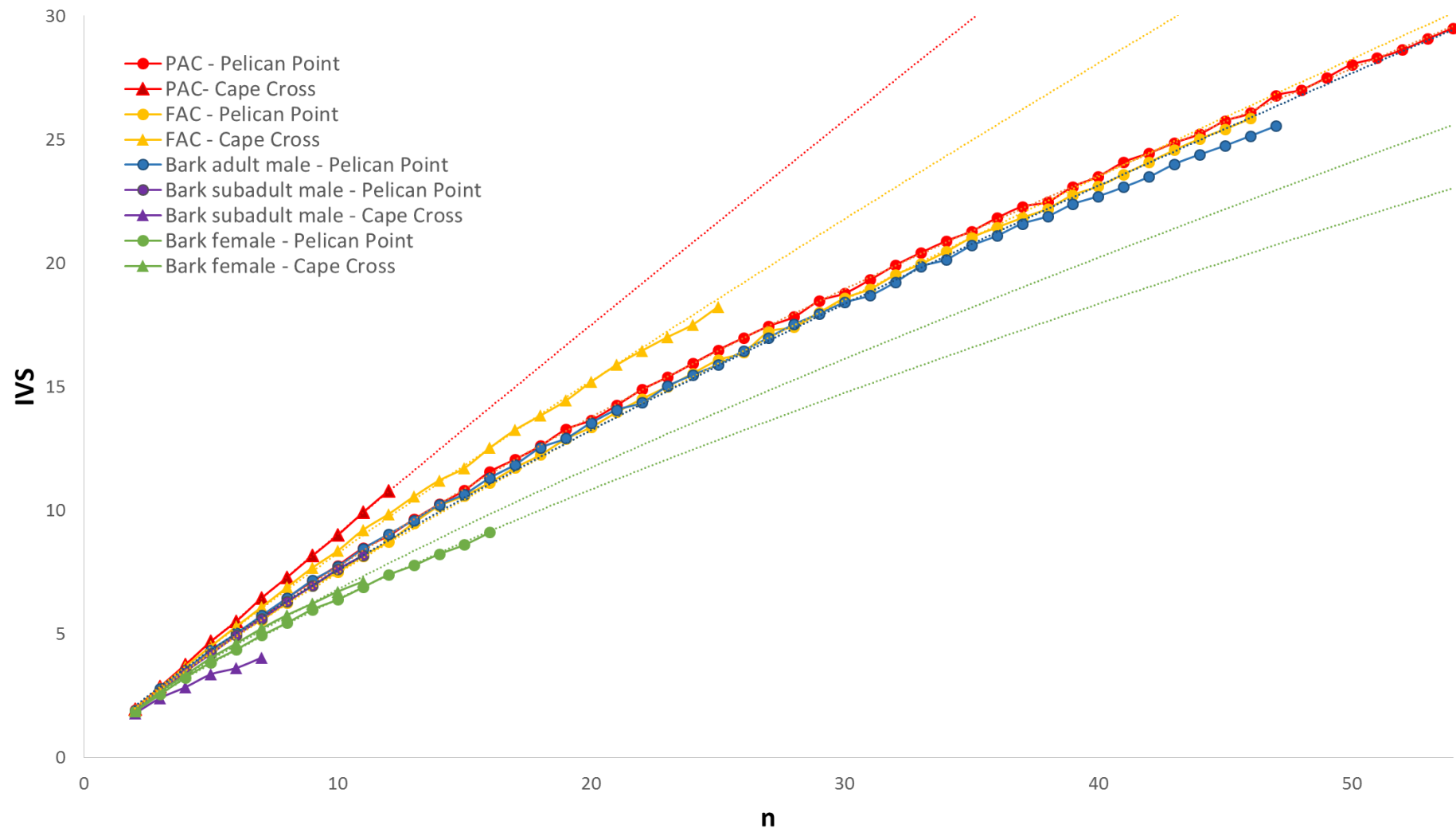
Fig. 3 Classification rates from Random Forest in female-attraction calls (FACs) according to pups' age-classes with a balanced classification method

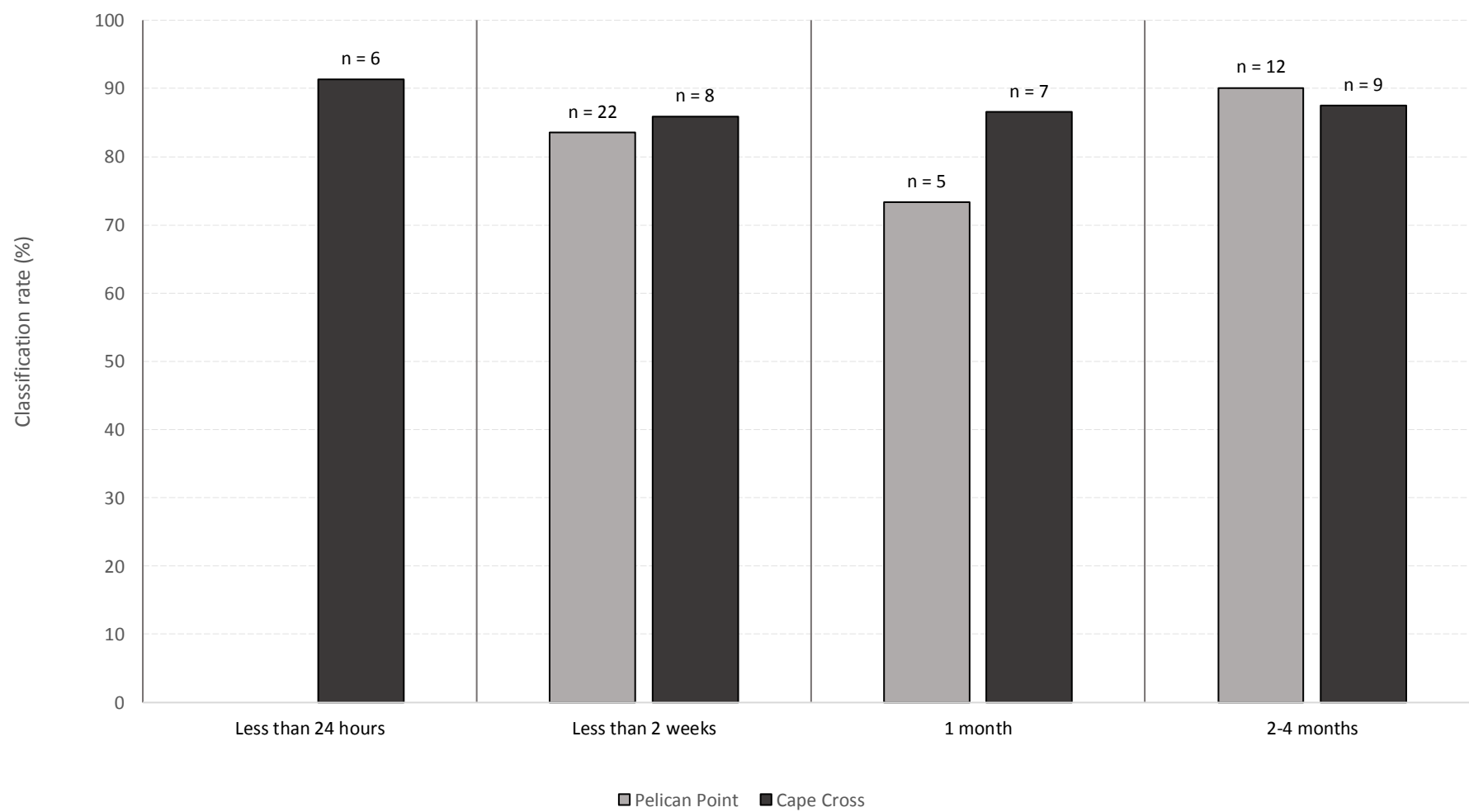
We randomly selected 5 individuals (i.e., *lowest sample size*) and performed a RF algorithm (number of trees: 1000 and number of variables at each node: 4). This procedure was repeated 100 times to mix selected individuals and include all the dataset.

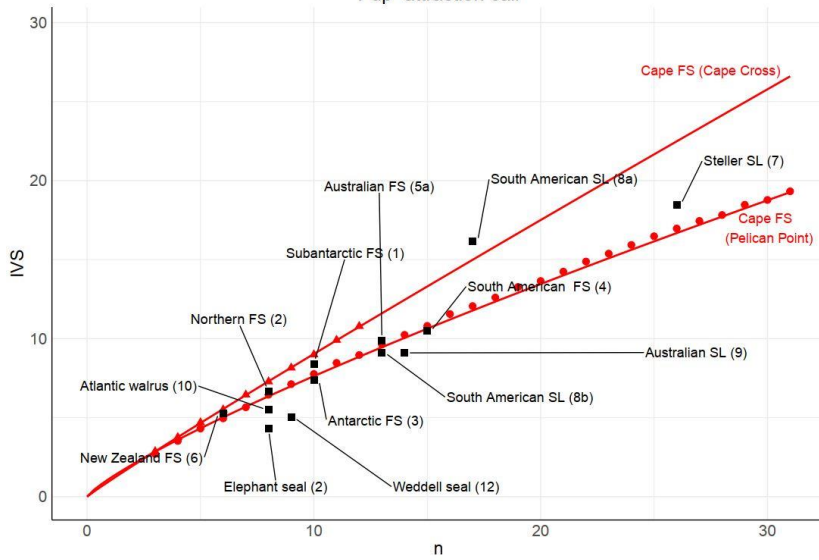
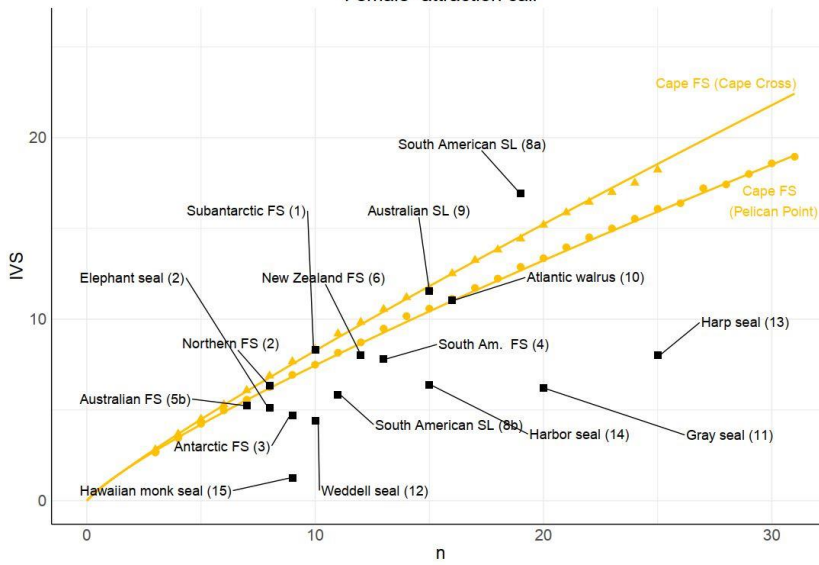
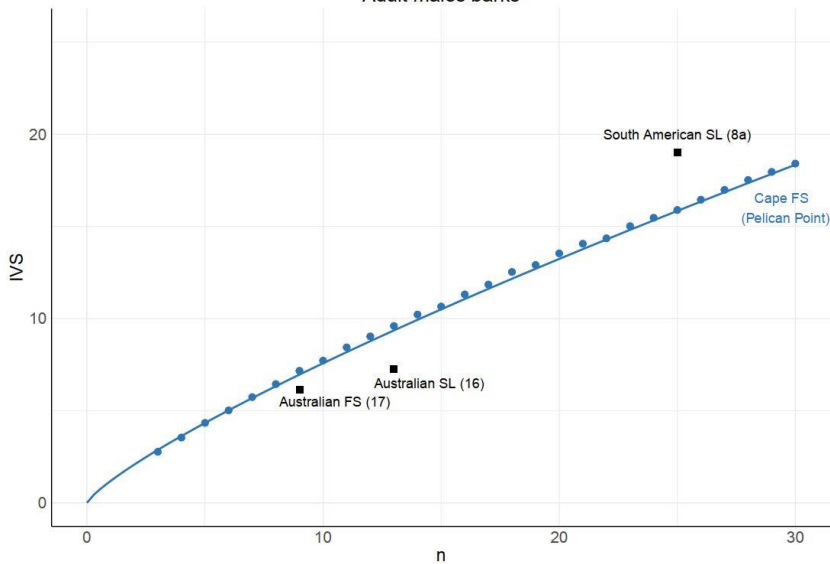
Fig. 4 IVS comparisons among pinnipeds species for three call types: Pup-attraction call (a), Female-attraction call (b) and Adult male bark (c)

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**Pup-attraction call****b****Female-attraction call****c****Adult males barks**



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