© 2024. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2024) 227, jeb246917. doi:10.1242/jeb.246917

RESEARCH ARTICLE

# Use of acoustic signals in Cape fur seal mother–pup reunions: individual signature, signal propagation and pup home range

**Mathilde Martin[1,2,*,‡], Tess Gridley[2,3], Antonia Immerz[4], Simon H. Elwen[2,3] and Isabelle Charrier[1]**

## ABSTRACT

The Cape fur seal (*Arctocephalus pusillus pusillus*) is one of the most colonial mammals, with colonies of up to hundreds of thousands of individuals during the breeding season. During the lactation period, mothers and pups are regularly separated as females undertake multi-day foraging trips at sea. Mothers and pups use a mutual vocal recognition system to reunite after separation. Such communication is highly constrained by both high background noise and risk of individual confusion owing to the density of seals. This study aimed to experimentally assess the acoustic features relevant for mother–pup vocal identification and the propagation properties of their calls. Playback experiments revealed that mother and pup individual vocal signatures rely on both temporal and frequency parameters: amplitude and frequency modulations, timbre and fundamental frequency ($f_0$). This is more parameters than in any colonial species studied so far. The combinational use of acoustic features reinforces the concept that both environmental and social constraints may have acted as selective pressures on the individual vocal recognition systems. Theoretical propagation distances of mother and pup vocalisations were estimated to be below the range of distances at which mother–pup reunions can occur. This suggests that Cape fur seals may have strong abilities to extract vocal signals from the background noise, as previously demonstrated in the highly colonial king penguin. Investigating the transmission of information throughout the propagation of the signal as well as the ability of the receiving individual to decipher vocal signatures is crucial to understanding vocal recognition systems in the wild.

**KEY WORDS: *Arctocephalus pusillus pusillus*, Individual vocal recognition, Pinnipeds, Playback experiments, Mother–young interactions, Vocal signature**

## INTRODUCTION

In mammalian species, one or both parents ensure their offspring's survival by providing care to them for a determined period of time, which varies in duration among species. This parental attendance period is often characterised by close communication between the caregiver(s) and their young (Trivers, 1974). Different types of information can be transmitted through different sensory channels (e.g. visual, olfactory or chemical). Besides dynamic information related to the internal state of the signal emitter (e.g. the offspring's hunger; Manser et al., 2008) or stress (Bartosova-Vichova et al., 2007) – likely to facilitate the initiation of appropriate parental behaviours or to enhance their effectiveness – static information about the caller's identity can be transmitted as well. Individual recognition is the process by which the receiver deciphers identity information to recognise a conspecific through its communication signals (Sherman et al., 1997). Individual recognition is a key component in parental care as it can reduce the risk of misdirected care and thus optimise parental investment (Halliday and Slater, 1983). This is particularly important in species where parents and offspring regularly separate and thus have a strong need for individual identification.

Acoustic signals such as the vocalisations produced by mammals are known to reliably encode individual information and allow individual vocal recognition (Carlson et al., 2020). An extensive body of research has documented the ability of mother and offspring to recognise each other through their vocalisations in a wide range of mammals (parental care is asymmetrical in many species and rearing of young is ensured by the mother in most cases), for instance, in non-human primates, rodents, bats, carnivores, ungulates and pinnipeds (for review, see Carlson et al., 2020). As proposed in Shannon and Weaver (1949), acoustic communication can be approximated to a three-step process. It involves the emission of information (encoded in a sound signal), its propagation through the environment, and its reception and decoding by a receiver. Most studies aiming to unfold vocal recognition systems focus on the first part of the process: the coding of individual information, i.e. the vocal individual stereotypy (also called 'individuality') in vocalisations (e.g. Sousa-Lima et al., 2002; Blumstein and Munos, 2005; Matrosova et al., 2011; Déaux et al., 2016). Yet, the consistency of reliable information throughout the propagation of the signal as well as the ability of the receiving individual to decode vocal signatures and to show an appropriate behavioural response are also crucial aspects to consider. Although a call type may display inter-individual variations on certain acoustic features, they are not necessarily involved in the recognition process by the receiver (McCulloch et al., 1999; Townsend et al., 2010; Wyman et al., 2022). Understanding which acoustic parameters are used by recipients to effectively identify a conspecific requires an experimental approach, including playback experiments using modified or synthesised signals (Deecke, 2006). Such investigations have been carried out on three pinniped species [the subantarctic fur seal, *Arctocephalus tropicalis* (Charrier et al., 2002, 2003a), the Antarctic fur seal, *Arctocephalus gazella* (Aubin et al., 2015), and the Australian sea lion, *Neophoca cinerea* (Charrier et al., 2009; Pitcher et al., 2012)], sheep (Searby and Jouventin, 2003; Sèbe et al., 2011), sulids and larids (Charrier et al., 2001; Dentressangle et al., 2012), and six penguin species (Aubin and Jouventin, 2002). Results showed that individuals generally integrate multiple acoustic parameters [e.g. frequency modulation (FM), amplitude modulation (AM), the spectral

---

[1]Institut des Neurosciences Paris-Saclay, Université Paris-Saclay, CNRS, 151 Route de la Rotonde, 91400 Saclay, France. [2]Sea Search Research and Conservation NPC, 4 Bath Road, Muizenberg, Cape Town 7945, South-Africa. [3]Department of Botany and Zoology, Faculty of Science, Stellenbosch University, Stellenbosch 7605, South Africa. [4]Mammal Research Institute Whale Unit, Department of Zoology and Entomology, University of Pretoria, 0028 Pretoria, South Africa.
‡Present address: Department of Evolutionary Biology and Environmental Studies, University of Zurich, 8057 Zurich, Switzerland.

*Author for correspondence (mathilde.martin@universite-paris-saclay.fr)

M.M., 0000-0002-9314-4729; T.G., 0000-0003-0925-5782; A.I., 0000-0002-9859-3558; S.H.E., 0000-0002-7467-6121; I.C., 0000-0003-4873-2342

**Received 21 October 2023; Accepted 31 May 2024**

content, the call frequency values] to decode individual signature, and the use of these acoustic features varies depending on the ecological constraints of the species. Indeed, species with high ecological constraints (i.e. highly colonial species without visual cues for reunion) typically use a more complex individual vocal signature offering more coding combinations that limits the risk of confusion among individuals (Aubin and Jouventin, 2002).

In the Cape fur seal, the social structure and maternal care strategies lead to high selective pressures for mother–pup recognition, making this otariid species an excellent mammalian model for the study of individual vocal signature. Indeed, each year during the breeding season (from mid-November to early January; Rand, 1967), females give birth to a single pup that they will nurse for a period of 9 to 11 months (David and Rand, 1986). Throughout this period, pups rely on their mother for food, as fostering or allo-suckling is uncommon in this species (Rand, 1955; Riedman, 1990). Additionally, otariid females are generally highly aggressive towards non-filial pups (Harcourt, 1992), leading to high costs for pups to approach non-mother females. The long lactation period is interrupted by regular separations between mother and pup, which necessarily requires their ability to reunite. Adult females undertake their first foraging trip at sea as early as 6 days after parturition (David and Rand, 1986). The mean duration of the first postpartum absence is 2.3 days and it increases progressively throughout the first 90 days (David and Rand, 1986). Mothers are absent from the colony approximately 70% of the time until weaning (Gamel et al., 2005). Mother–pup reunions are largely constrained by the number of animals and the density of individuals on breeding colonies. As one of the most colonial mammal species in the world, Cape fur seal breeding colonies are annually composed of tens of thousands of individuals and can reach up to 210,000 seals as in Cape Cross in central Namibia (Ministry of Environment and Tourism, 2024). During this period, fur seals are extremely vocal and use acoustic signals in all their social interactions such as territorial defence, mating, agonistic interactions or mother–pup communication (Martin et al., 2021a). Fur seal colonies are therefore a noisy environment in which the risk of visual and acoustic confusion is particularly high. However, acoustic signals play a major role in mother–pup reunions (Martin et al., 2022a,b). Mother and pup use vocalisations to recognise each other, correspondingly named ‘pup-attraction calls’ (PACs) and ‘female-attraction calls’ (FACs), which are produced with a clear harmonic structure and a mean duration of 1118 and 637 ms, respectively (Martin et al., 2021a). PACs are lower-pitched than FACs, with average fundamental frequency values of 270 Hz compared with 372 Hz (Martin et al., 2021a). These two call types display a high degree of vocal stereotypy, mostly encoded in their duration, spectral features and FM pattern (Martin et al., 2021b). Experimental investigations confirmed a mutual mother–pup vocal recognition (Martin et al., 2022b). Such recognition is established remarkably early after the pup’s birth: females recognise their pup’s calls between 2 and 4 h after parturition and pups develop this ability when they are 4 to 6 h old (Martin et al., 2022a). Two aspects of the mother–pup vocal recognition process remain to be studied in this species: (1) the propagation of PACs and FACs as well as the reliability of the individual information transmission, and (2) the decoding process of the individual identity.

This study aimed to increase our understanding of the entire chain of transmission of individual information between Cape fur seal mothers and pups. Considering the high ecological constraints for mother–pup vocal recognition in this species, we expect to find a more complex individual vocal signature compared with those found in other colonial species studied so far. To test this hypothesis, we first performed playback experiments on mothers and pups using modified signals to assess the acoustic features involved in the identification process, and to test whether the individual vocal signature is more complex than those previously found in other highly colonial species. Second, we evaluated the acoustic degradation undergone by PACs and FACs during their propagation throughout the natural environment of Cape fur seals. Propagation tests allowed us to assess the reliability of the vocal signature as well as the constraints faced by the mother and her young during reunion events. Finally, the home range of the pups was estimated using GPS tags on pups, providing an indication of the surface area in which mother–pup reunions occur.

## MATERIALS AND METHODS

The study took place at the Pelican Point Cape fur seal breeding colony, Namibia (25°52.2′S, 14°26.6′E), during the 2021 and 2022 breeding seasons (experiments performed between November and January). Pelican Point is a dynamic sandy peninsula with a uniform and flat topography enclosing the Walvis Bay lagoon. Cape fur seals (Schreber 1776) occur all around the peninsula and extend from the shoreline to 20 to 100 m inland, depending on the time of day and tidal movements. The present study was conducted on the eastern side of Pelican Point as this area has low exposure to waves and swell because it borders the lagoon, not the open ocean, giving easier access to animals.

All procedures were approved by the Research Ethics Committee (Animal Care and Use) of Stellenbosch University (ACU-2021-15015) and authorized by the Namibian National Commission on Research Science and Technology (NCRST; authorization no. AN202101095).

### Individual vocal signature

Vocal signature was investigated through playback experiments performed between mid-November 2021 and early January 2022 and between mid- and late November 2022. We tested a total of 41 mother–pup pairs in 2021–2022 and 52 in November 2022 for which we could test either the female, the pup or both.

#### Markings

To identify mother–pup pairs over time, we used the same procedure previously used on Cape fur seal mother–pup pairs (Martin et al., 2022a, b), which is very common for pinniped marking. Pups were bleach-marked using hair dye (Blonde highlight kit, Kair). Marks consisted of numbers applied on their flank using a 10-cm-wide wooden pad attached to a 5-m-long pole. This procedure is performed at a distance, and is minimally invasive. A potential disturbance was further reduced by not marking the females. These were identified through the association with and/or nursing of their marked pup. Indeed, adoption is extremely rare in otariid species (Riedman, 1990), and the association of pups with their mother is very clear to determine as fur seal females are aggressive towards non-filial pups (Harcourt, 1992).

#### Acoustic recordings

PACs and FACs were recorded when mothers and pups were calling for each other, and they are the only call types used during mother–pup vocal exchanges (Martin et al., 2021a). We used 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 digital audio recorder. Distance from focal animals ranged from 3 to 6 m during recording sessions.

#### Playback stimuli design

One good-quality call was selected for each individual (either PACs from females or FACs from pups). We selected calls through visual inspection of our recordings in a spectrogram, and included only calls without any overlap with another calls (other seals) or background noise (wind, waves).

For each selected call, a 100 Hz high-pass filter was applied. PACs and FACs were not altered by the filtering because their average fundamental frequency is higher than 100 Hz (264±41 Hz for PAC and 364±79 Hz for FAC, Martin et al., 2021a). A spectrogram was generated in Avisoft SAS Lab Pro (R. Specht, version 5.3.02, Avisoft Bioacoustics, Berlin, Germany) with a 1024-point fast Fourier transform (FFT), 87.5% overlap and a Hamming window (frequency resolution=22 Hz). To create modified signals used in the playback experiments, the raw calls were re-synthetized using the Synthesizer function in Avisoft by applying the ‘scan frequency contour and amplitude envelope’ and ‘scan harmonics from spectrogram based on fundamental’ functions to the raw signal. The number of harmonics chosen was between 10 and 24 depending on the call to best reflect the voice spectral characteristics. The resulting synthesized signal served as a control signal and allowed further modifications (Fig. 1). To ensure that the raw and the synthetized signals were highly similar, we performed a spectrogram cross-correlation using the Avisoft correlator function. Correlations were made with a tolerance of 10 Hz for females and 20 Hz for pups (values based on the intra-individual variation of the fundamental frequency in Cape fur seal PACs and FACs; Martin et al., 2021a).

The modifications of acoustic signals used in this study are similar to those used in previous studies investigating individual vocal signatures in both colonial birds and pinnipeds (Aubin and Jouventin, 2002; Aubin et al., 2015; Charrier et al., 2002; Charrier et al., 2003a,b). Five distinct modifications were applied to the control signal to create five additional experimental signals by varying the fundamental frequency ($f_0$), the energy distribution, as well as AM and FM patterns. The first consisted of applying an upwards linear shift to the control call’s fundamental frequency value of 10 Hz for female vocalisations and 20 Hz for pup vocalisations (signals called +10 Hz and +20 Hz; Fig. 1). These values corresponded to limits of the natural intra-individual variation of the fundamental frequency measured in PACs and FACs (Martin et al., 2021b). The second consisted of an upwards linear shift of the fundamental frequency by 50 Hz for both PACs and FACs (signal +50 Hz; Fig. 1), which was a change well beyond the natural intra-individual variation, but still within the inter-individual variation (Martin et al., 2021b). All of these shifted signals had similar energy spectra among harmonics and similar modulation patterns to the control signal but a higher overall pitch. The next two modifications were related to AM and FM patterns of the calls. A signal called NoAM was created by removing the modulation on the relative amplitude of the fundamental and all harmonics, but did not alter the FM pattern (Fig. 1). A NoFM signal was built by removing the FM of the fundamental frequency and by keeping the natural envelope of the raw call, resulting in a ‘flat’ signal (Fig. 1). The last modification was performed on the spectral content, and consisted of randomly switching the energy levels of each harmonic within the overall spectrum (ModSpectr; Fig. 1). The order of the energy levels relative to each of the harmonics was thus changed according to a random sequence (generated by the function ‘sample’ from the ‘base’ R package, https://www.r-project.org/) going from 1 to the total number of harmonics of the call (i.e. between 10 and 24).

A playback track was created for each of the six stimuli: control, +10 Hz (or +20 Hz), +50 Hz, NoAM, NoFM and ModSpectr. A playback track was made with three repetitions of the same synthetic signal, each separated by 2 s of silence. Tracks had an average duration of 9.8±1.7 s for female and 7.3±1.2 s for pup vocalisations.

### Playback procedure

Each playback series consisted of exposing one focal individual, either female or pup, to a playback track. Females were tested in the presence of their pup, whereas pups were tested alone (female briefly absent for thermoregulation in the water or undertaking a multi-day foraging trip at sea). The loudspeaker was positioned within 1 to 3 m of the focal individual by crawling as close as possible and using a 5-m-long pole. We ensured a 45–90 deg angle between the loudspeaker and the focal individual’s head to induce head movement and facilitate the evaluation of its reaction during the playback. Calls were broadcasted using a waterproof and wireless high-powered loudspeaker (JBL Charge 3, 2×10 W, frequency response: 65 Hz–20 kHz) connected to a Bluetooth sound player (Roland R-07). Both the volumes of the sound player and the loudspeaker were calibrated on-site for a consistent

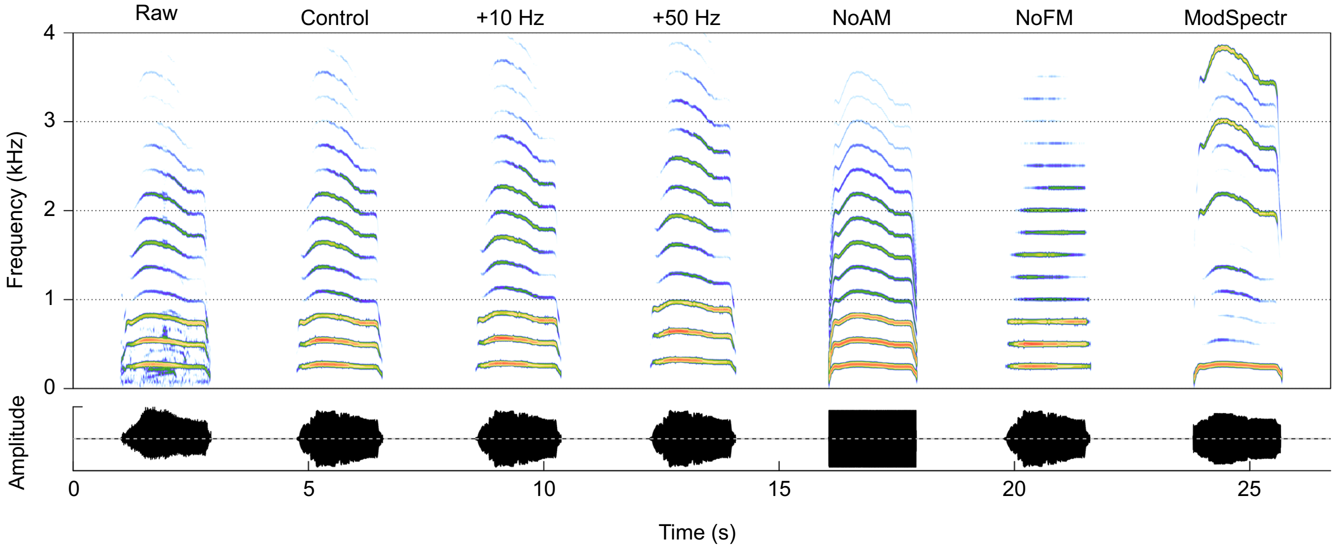

**Fig. 1. Spectrograms of the raw and control versions as well as the five modified signals from a pup-attraction call (produced by ‘female 91’ in 2021).**

broadcast amplitude among playback series. Stimuli were broadcasted at the natural amplitude of PACs and FACs, 88±2 and 80±2 dB SPL at 1 m, respectively (Martin et al., 2022b). Before each playback series, we ensured that the focal individual appeared calm and was not engaged in any social interaction or actively searching for their mother (for pups) or pup (for females) (i.e. pups or mothers calling and/or moving in the colony). All playback experiments were filmed using an Olympus Tough TG-6 camera to allow further analysis.

Females and pups were always first exposed to the control series (i.e. their pup or mother's call synthesized with original acoustic features) to test their responsiveness. In the case of no behavioural response to this first series, the session was stopped and another test was performed after at least 2 h had passed or during the following days. We started the new session again with the control series. This avoided including animals that were awake but not motivated to respond to our playback signals or sleeping too deeply to be awakened by the playback series. In such cases, these tests were excluded as we cannot conclude anything from them.

Although the ability of mothers and pups to recognise each other through their vocalisations has been demonstrated in this species (Martin et al., 2022b), we ensured that individuals included in the present study were capable of doing it. For this purpose, we compared the behavioural response of some females and pups when exposed to calls from a stranger individual (i.e. a non-filial pup or a non-mother female) and when exposed to filial or maternal calls. The stranger series consisted of a playback track randomly selected from our playback track database.

All animals demonstrating a strong behavioural reaction to the control playback series (i.e. a prolonged look towards the loudspeaker and/or vocal response, assessed *in situ* during the stimulus broadcast) could be tested with other series. During a session, individuals were exposed to up to seven series: the control series (always broadcast first) followed by the five different series of modified calls and the stranger series. The presentation order of the latter six series was random and differed among tested individuals. We waited at least 5 min between two consecutive series so that the tested animals went back to their baseline behaviour. If not all the series could be broadcasted consecutively in one session (e.g. the focal individual left), the remaining series were broadcasted later in the day or in the following days.

### Behavioural response

Responses to the playback series were all assessed through video analysis with the software BORIS (Friard and Gamba, 2016). Behavioural responses were observed for 20 s from the beginning of the playback (Martin et al., 2022a,b). For experiments conducted on mothers, response variables were latency to look towards the loudspeaker (s), look duration towards the loudspeaker (s), latency to call (s) and number of calls produced. As some tested pups were young (six were 6 days old or less), the behavioural response of pups was evaluated through their vocal production only. Indeed, newborn pups are not able to locate the sound source accurately and do not look towards the loudspeaker or approach it during playback experiments (Martin et al., 2022a). Response variables for pups were thus latency to call (s) and number of calls. For both mothers and pups, the absence of a given behavioural variable was assigned a default value of 20 s for latency.

### Statistical analysis

Similar to what was done for a study on Cape fur seal mother–pup vocal recognition (Martin et al., 2022a), the overall behavioural response of each tested individual was obtained by combining the raw data of the response variables (four for mothers and two for pups) in a principal component analysis (PCA). This method allows us to obtain a composite score (McGregor, 1992) and facilitate the interpretation of the behavioural response of tested individuals to playback series. Principal components (PCs) with eigenvalues greater than 1 were retained (Kaiser's criterion) and the corresponding PC scores were used to quantify the level of response of tested individuals. PC scores were thus compared between the control series and each of the experimental series (modified calls and stranger) using a linear mixed-effects model (LME). PC scores were set as a response variable, and the series was set as a fixed effect. The tested individual was defined as a random effect to account for the fact that data are non-independent (the same individual was tested with several experimental series). The model was run with the lme4 R package (Bates et al., 2015). A *post hoc* analysis of estimated marginal means was conducted using the emmeans package (https://CRAN.R-project.org/package=emmeans) and a Dunnett's correction was applied to correct for the comparison of multiple treatments (modified and stranger series) with a common control group (control series).

For both females and pups, we investigated a potential effect of the series order on the strength of the behavioural response. As control series were always performed first (to ensure a good motivation of the target animal), we excluded those series and performed an LME with PC scores as the response variable and the series order as a fixed effect. The tested individual was defined as a random effect. *P*-values were obtained using the car package (Fox and Weisberg, 2019).

### Signal propagation tests

To assess the degradations of vocalisations undergone during propagation throughout the colony, we performed propagation tests using three different calls: a PAC produced by a female, a FAC from a bleating pup and a FAC from another pup without bleating. The bleating (or quavering) is a fast frequency modulation commonly found in fur seal calls (Charrier et al., 2003b; Martin et al., 2021a; Tripovich et al., 2009). With age, the number of bleating pups tends to decrease, as well as the proportion of bleating within their calls (Martin et al., 2021a). For each of the three signals, one good-quality call (low background noise and no overlap) was selected and repeated 20 times (with a 2 s silence interval) to build a propagation playback track. At the beginning and the end of each track, a synthetic sound showing an inverted V-shape frequency modulation (0.2–2 kHz) was added to help in the time-synchronisation of the recordings. These sequences were broadcast with a loudspeaker (characteristics detailed above) at the natural amplitude level (as described above) and re-recorded with the built-in microphone of an Edirol R-09 digital recorder (sampling frequency=44.1 kHz; frequency response: 20 Hz–22 kHz) at six distances: 1 m (control), 8 m, 16 m, 32 m, 64 m and 128 m. Recording distances were measured with a Garmin GPSMAP 65 Handheld GPS. This testing procedure was carried out away from the colony (approximately 200 m away from the nearest seals), in a quieter area of Pelican Point but showing the same environmental characteristics. Tests were performed under calm weather conditions (sunny, no wind) and the loudspeaker and the microphone were placed approximately 30 cm above the sand. This experimental procedure allowed us to assess the theoretical distance beyond which an acoustic feature does not transmit reliably in the environment.

On the tracks we recorded at various distances, we manually selected 10 calls (of the 20) with no overlap with any other signal from the environment. Each of these calls was individually analysed in three ways as we built the spectrogram, the amplitude envelope and the amplitude spectrum using Avisoft SAS Lab. Using these three different analyses, we investigated the FM pattern, the AM pattern and the frequency content (timbre) of the calls, respectively. Spectrograms were built using the following parameters: Hamming window, FFT length=1024, frame size=100% and overlap=87.5%. Amplitude envelopes were built with a 101-point smooth (corresponding to 4.58 ms). Amplitude spectra were created on the range 0–6 kHz with a 31-point smooth (corresponding to 20 Hz). We used the Avisoft correlator function to calculate correlations between the control series (1 m) and the propagated series (recorded at 8, 16, 32, 64 or 128 m) for each of the three types of analysis (spectrograms, amplitude envelopes and amplitude spectra). For spectrogram correlations, we set a tolerance of 10 Hz for females and 20 Hz for pups (intra-individual variation). Correlation coefficients were returned in a correlation matrix for each of the comparisons between the 10 calls of the control series and the 10 calls of the propagated series. The acoustic similarity between the control and a propagated sequence was determined as the average of inter-sequence correlation coefficients for each pairwise comparison. We set an average correlation coefficient of 0.5 as a threshold to distinguish reliably propagated signals from degraded ones and assess the maximum distance over which individual identification remains reliable.

## Pup on-land home range

### GPS tags and accuracy tests

Pups were equipped with small GPS tags in order to track their movements on the colony and assess the size of their home range. We deployed 10 CatLog Gen 2 GPS/GNSS Loggers (Perthold Engineering LLC) each year during the two consecutive 2021–2022 and 2022–2023 breeding seasons. In 2021–2022, tags were coated in a heat-sealed enclosure and measured 2.5×6×1 cm. For the next year, we used the same devices potted in Epoxy resin, for a size of 4.5×4.5×1 cm. The base of the tags was covered with a thin layer of neoprene attached with cable ties in order to enable a quick release. The accuracy of the data points recorded by the tags was assessed at Pelican Point. Two tags were placed for 3 and 4 h at a fixed location where the GPS point was recorded by a Garmin GPSMAP 65 Handheld GPS (reference point). The distance between the points (recorded every minute) and the reference point was measured over the entire recording period for the two tags.

### GPS tag deployment procedure

Pups were selected according to their age and body condition. First, we ensured that they were at least 6 days old by selecting previously marked pups for which we knew the exact date of birth or pups on which we made sure the umbilical cord had fallen off completely (previous observations showed that the umbilic cord remains on pups for about a week at Pelican Point). Second, pups had to be larger and heavier than the average pups seen in the area. Pups were captured by hand in the absence of their mother and taken away from the other seals (approximately 20 m away). This enabled us to kneel during the tag deployment, limiting the disturbance for the seals as they became agitated when we stood up tall. It also allowed us to work in safety, away from adult seals that might come and check on us. Tags were placed at the bottom of their back, at the level of their hips and approximately 10 cm anterior to the tail. This prevents the tag from being uncomfortable when they are laying on their back. The neoprene layer covering the base of tags was glued directly to the pups' hair with quick-setting epoxy glue (RS Component, France). As the hair was relatively long, the glue did not reach the skin. The pups were gently restrained while the glue set, approximately 7–8 min in total. During that time, we used hair dye to apply a unique mark on their flank to facilitate daily monitoring. At the end of the procedure, pups were released at the exact location where they were caught. The retrieval of the tags was also carried out in the absence of the mother. This procedure did not always require catching the pups as we only had to cut the cable ties to detach the tag from the sleeping animal. The thin layer of neoprene was left on the animal and fell off naturally during moulting.

### GPS data analysis

In 2021–2022, tags were set to record a GPS location every 30 min, whereas in November 2022, tags were set to record every 10 min. First, the data were cleaned to eliminate outliers. Outliers were defined as points ($p$) for which the distance between this point and the previous point ($p$–1) and the distance between this point and the next point ($p$+1) were both greater than 300 m for the 2021–2022 data and greater than 100 m for the November 2022 data. For each pup, we estimated its overall home range (i.e. the area the pup covered) over the entire period of GPS recording. For reasons of simplification, we considered the home range to be an ellipse drawn at 95% confidence level for a multivariate $t$-distribution. We used the length of the major axis (in m) as an estimation of the size of pups' home range. The same method was used to calculate the size of the pups' daily home range by looking at data separately for each recorded day. Finally, the distance between two consecutive daily home ranges was evaluated by calculating the distance between the centroids of the two ellipses. Home range analyses were performed in R with the package geosphere (https://CRAN.R-project.org/package=geosphere).

The size of the daily home range of the pups was investigated in relation to maternal attendance. The presence or absence of a mother with her pup was monitored as much as possible during the GPS recording period of the pups. If a pup was seen at least once with its mother within the day, the mother was considered present. If the mother was not seen at all during the day, she was considered absent. A generalized linear mixed-effects model (GLME) assuming a binomial distribution was fitted with the size of daily home range as a fixed effect, the presence/absence of the mother as the response variable and the pup ID as a random effect. $P$-values were obtained using the car package (Fox and Weisberg, 2019). Secondly, we assessed whether the size of pups' daily home range varied over the GPS recording period. A linear regression was fitted between the size of daily home range and the recording day for each deployment.

## RESULTS

### Individual vocal signature

Of the 93 mother–pup pairs marked and recorded (41 in 2021–2022 and 52 in 2022), 19 mothers and 23 pups from 37 different pairs could be tested with at least two playback series (including the control) and were included in the analysis. Three females and three pups were tested with the control series only and were thus excluded. A total of 15 mothers and 23 pups showed no behavioural response to the first control series, i.e. they did not look at the loudspeaker, did not call or did not move during the playback (response evaluated in real-time by the experimenters). In these cases, the playback experiment was stopped and the test was performed again after a minimum time period of 2 h or during the following days. Of the 23 pups included in the study, the exact date of birth was known for 18 pups: six were less than 6 days old, nine were between 7 and 21 days old, and three were older than 21 days. The age of five remaining pups could not be estimated accurately but they were older than 6 days (no umbilical cord remains, Martin et al., 2022b).

Spectrogram correlations between raw and synthetic (control) signals had mean±s.d. correlation coefficients of 0.93±0.07 for PACs ($n$=19) and 0.83±0.08 for FACs ($n$=23). For both mother and pup playback experiments, only the first principal component (PC1) had an eigenvalue greater than 1 and was retained (Table 1), explaining 65.74% and 89.78% of the total variance, respectively. In both cases, PC1 was highly correlated with all response variables (four for mothers and two for pups; Table 1).

For mothers, positive values of PC1 scores corresponded to strong behavioural responses: short latencies to look towards the loudspeaker or to call back, prolonged look and numerous calls produced in response. In contrast, negative values of PC1 scores were characterised by long latencies and no or little vocal production. Mothers responded more strongly to the calls of their own pup (control) than to those of a non-filial pup (stranger; Fig. 2), confirming the occurrence of individual vocal recognition of the pup by mothers (Martin et al., 2022b). No significant differences in mothers' behavioural responses were found between control and the experimental signals +20 Hz and NoAM series (Fig. 2). In contrast, the experimental signals +50 Hz, NoFM and ModSpectr series elicited weak reactions, and those were significantly different to those obtained with the control (emmeans *post hoc* $P$=0.0001–0.0329) (Fig. 2).

For pups, negative values of PC1 scores were associated with a strong vocal response, i.e. short latency to call and numerous calls produced, whereas positive scores illustrated a total absence of vocal response. As with their mothers, pups showed stronger reactions to their mother's calls (control) compared with those from non-mothers (stranger; Fig. 2), confirming the recognition of their mother's voice, as previously shown (Martin et al., 2022b). Pup behavioural responses were strong for both the control and +10 Hz series, and no difference occurred between the two (Fig. 2). However, they responded significantly less (higher PC1 scores, $y$-axis reversed on pups' response plot; Fig. 2) to the four other experimental series: +50 Hz, NoAM, NoFM and ModSpectr (emmeans *post hoc* $P \leq 0.0001$). For NoAM and NoFM series, pups' reactions were highly variable among individuals, with some pups showing PC1 scores similar to those found for the control or +10 Hz series (Fig. 2). The proportion of pups that vocally responded to the playback (production of at least one call during the 20 s observation period) is represented for each series in Fig. 3 (number of calls produced and latencies are shown in Table S1). Of the 23 pups tested with the control series, all of them called back in response to the playback. More than 75% of tested pups called in response to the +10 Hz series as well. For NoAM and NoFM, about half of the pups produced calls and only about 25% for the stranger, +50 Hz and ModSpectr series (Fig. 3).

In both female and pup playback experiments, no effect of the presentation order of the series was found on the tested individual's behavioural response. This suggests the absence of habituation and excludes a possible bias owing to consecutive exposures to playback stimuli.

**Table 1. Summary of the first principal component (PC1) resulting from the two principal component analyses performed on mother and pup playback experiments**

| | Playbacks on mothers PC1 | Playbacks on pups PC1 |
|---|---|---|
| Eigenvalues | 2.63 | 1.80 |
| % Cumulative variance | 65.74 | 89.78 |
| Correlation coefficients between PC and variables | | |
| Latency to look | −0.65 | |
| Look duration | 0.84 | |
| Latency to call | −0.86 | 0.95 |
| Number of calls | 0.88 | −0.95 |

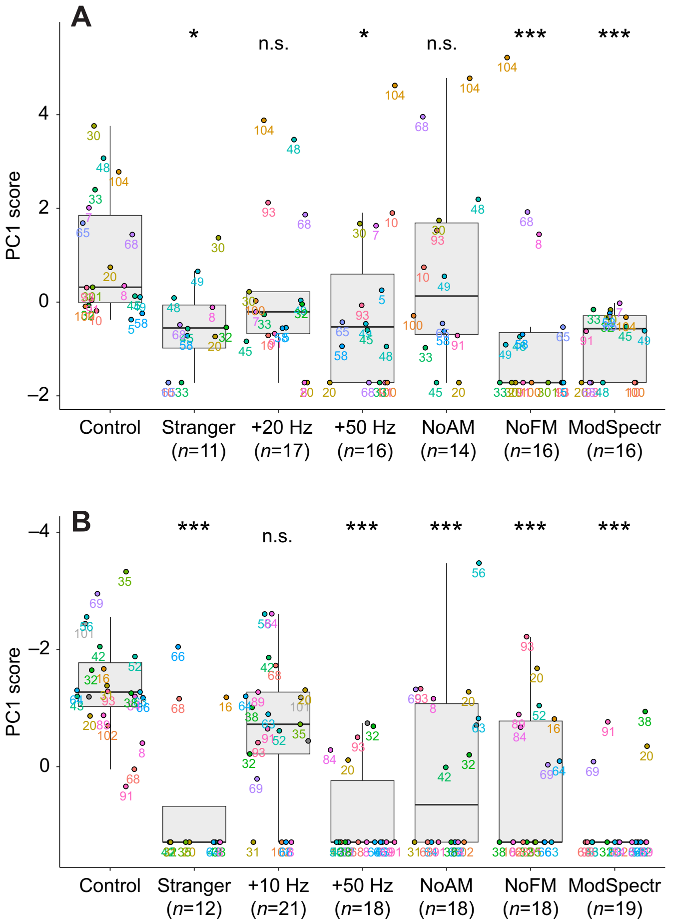

**Fig. 2. Behavioural response of mothers and pups (indicated by PC1 scores) to each of the playback series.** (A) Experiments on females; (B) experiments on pups. Statistical test: LME followed by an estimated marginal means *post hoc* analysis including a Dunnett's correction for comparison of multiple series (stranger and modified calls) with a common control series (***$P$<0.001; *$P$<0.05; n.s., not significant). Boxplots present median values with first and third quartiles (lower and upper hinges) and the interval between the smallest and the largest values (whiskers, no further than 1.5×IQR from the hinge). For the pups' response plot, the $y$-axis is reversed because highly negative values correspond to a strong behavioural response. Coloured numbers represent individuals.

### Signal propagation tests

The maximum propagation distance in the breeding colony was estimated for one PAC and two FACs (Fig. 4) by investigating three aspects of their acoustic structure. Correlation coefficients resulting from spectrogram, amplitude envelope and amplitude spectrum correlations were calculated for comparisons between the control series (1 m) and propagated signals recorded at a distance of 8, 16 and 32 m. Signals recorded at 64 and 128 m were fully confounded in the background noise and could not be extracted with confidence (the inverted V-shape signal could not be discerned either).

Average spectrogram correlation coefficients were greater than 0.5 for the three signals recorded at 8 m (Fig. 4). At this distance, PACs showed a greater coefficient (0.78) than FACs, with FACs with bleating having greater spectrogram correlations (0.61) than FACs without bleating (0.51) (Fig. 4). At longer distances, spectrogram correlation coefficients of the three signals decreased drastically between 8 and 16 m, reaching less than 0.3 at 16 and 32 m (Fig. 4). The amplitude spectrum correlation coefficient was

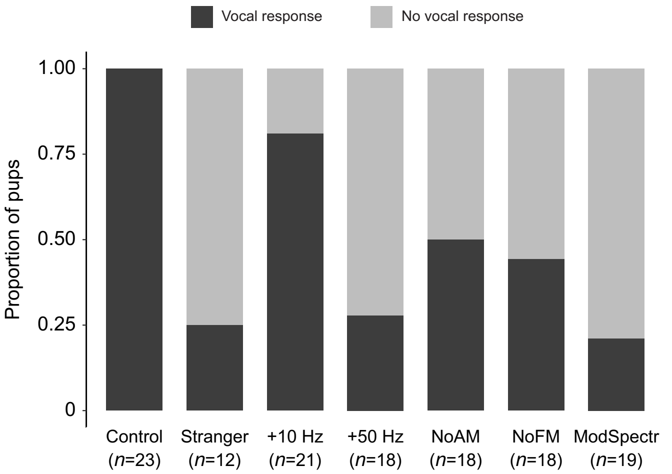

**Fig. 3. Proportion of pups showing a vocal response during the broadcast of the different tested signals.**

greater than 0.5 for the PAC at 8 m only (0.58 against 0.4 and 0.37 for the two FACs; Fig. 4). The coefficients resulting from the amplitude envelope correlations were all lower than 0.3 regardless of the call type and the propagation distance (Fig. 4).

### Pup on-land home range

Accuracy testing of the GPS tags at Pelican Point showed that, based on the 392 positions recorded by the two tags, they were on average 18 ±18 m away from the reference position, indicating an approximate accuracy distance of 18 m at Pelican Point study site.

A total of 21 GPS tag deployments were performed on different pups in November 2021 and November 2022. Of these, two were lost (pups died and/or moved beyond range) and one was redeployed following the death of the initial tagged pup after 8 days. From the resulting 19 exploitable data sets, five had GPS recording durations shorter than 6 days (mostly due to technical issues with the waterproofing of the tags) and were thus excluded from analysis. Data from the 14 successful deployments were analysed and provided information on the overall and daily home range sizes for each of these tagged pups (Table 2). Among all deployments, less than 3% of the recorded were considered as outliers and removed from the datasets.

All pups were seen with their mother at least once during the GPS recording period, except P14. This is the only pup that was left alone for the entire period and was found dead 8 days after the tag deployment. The distances travelled by this individual were much greater than those travelled by the other pups. It appears that P14 was actively searching for his mother in the colony during the last few days of GPS recording, probably because the pup was starving. As this situation was exceptional, the home range data for P14 were not included in the calculation of mean values to avoid biasing the results.

Results reported that, over the whole recording period (ranging from 6 to 35 days depending on the deployments), pups wandered in an area – considered to be ellipsoidal – of ∼66±18 m of the major axis (Table 2, Fig. 5). Their daily home ranges had similar sizes, measuring 60±36 m (major axis) on average (Table 2). From one

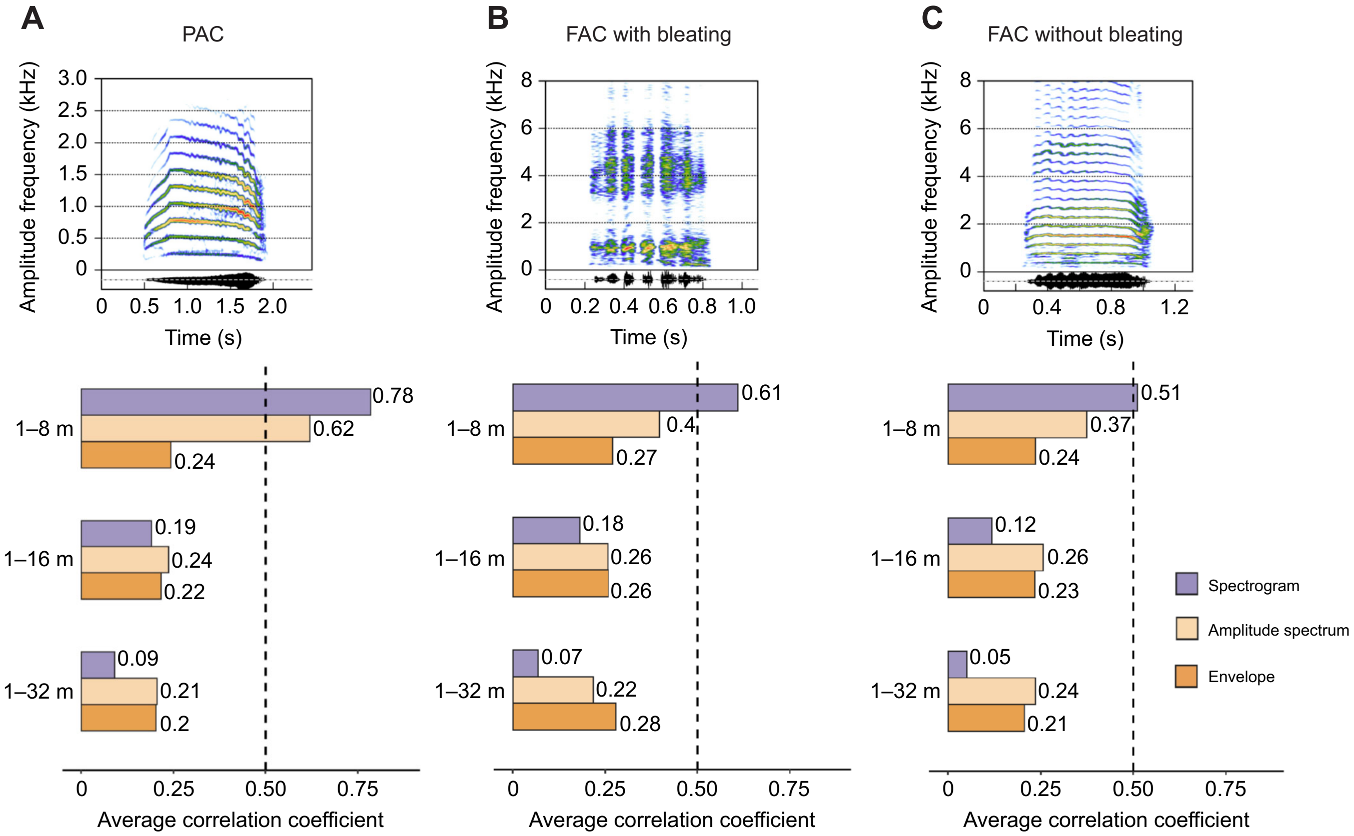

**Fig. 4. Correlation coefficients for the pairwise analyses between the control (1 m) and propagated signals recorded at different distances (8, 16 and 32 m) performed on the spectrogram, the amplitude spectrum and the envelope of three call types and spectrograms of the three signals used for the propagation tests.** (A) Pup-attraction call (PAC). (B) Female-attraction call (FAC) with bleating. (C) FAC without bleating. Spectrograms were generated using Seewave (Sueur et al., 2008) (Hamming window, FFT length: 1024, 90% overlap).

**Table 2. Summary of pup home range results for each deployment of GPS tags during the two breeding seasons (November 2021 and November 2022)**

| Pup ID (deployment date, dd-mm-yy) | Pup age (days) | Pup sex | GPS recording duration | Size of overall home range (m) | Mean±s.d. size of daily home range (min.–max.) (m) | Mean±s.d.distance between two consecutive daily home ranges (m) |
|---|---|---|---|---|---|---|
| P14 (15-11-21) | | M | 8 days 6 h 7 min | 159 | 158±156 (26–441) | 40±32 |
| P39 (23-11-21) | | F | 12 days 8 h 29 min | 43 | 44±15 (17–68) | 9±4 |
| P33 (23-11-21) | | M | 26 days 22 h 11 min | 67 | 66±27 (27–141) | 10±6 |
| P51 (26-11-21) | | F | 29 days 21 h 36 min | 82 | 69±48 (20–240) | 14±12 |
| P31 (21-11-21) | | F | 35 days 23 h 11 min | 96 | 84±53 (23–244) | 18±19 |
| P10 (12-11-22) | 7 | F | 15 days 22 h 51 min | 88 | 50±16 (31–83) | 20±20 |
| P29 (17-11-22) | 8 | F | 10 days 19 h 16 min | 62 | 47±18 (21–85) | 15±7 |
| P38 (18-11-22) | 6 | M | 9 days 5 h 14 min | 43 | 42±14 (18–58) | 12±6 |
| P52 (18-11-22) | | F | 9 days 18 h 23 min | 42 | 39±10 (27–55) | 13±5 |
| P53 (18-11-22) | | F | 9 days 22 h 28 min | 84 | 58±28 (21–114) | 23±11 |
| P62 (20-11-22) | | F | 7 days 22 h 36 min | 67 | 58±10 (36–71) | 17±14 |
| P63 (20-11-22) | | F | 7 days 1 h 41 min | 63 | 55±12 (38–69) | 12±10 |
| P8 (21-11-22) | 16 | M | 7 days 2 h 15 min | 72 | 56±12 (35–74) | 15±14 |
| P35 (21-11-22) | 10 | F | 6 days 22 h 3 min | 46 | 39±5 (33–45) | 17±8 |
| Mean±s.d. | | | | 66±18 | 60±36 | 15±13 |

P14 is highlighted in grey as this deployment was excluded from the analysis.

day to the next, the position of the home range centroid moved 15 ±13 m on average (Table 2).

No difference in the size of the pups' home range was found whether the pup was with its mother or alone in the colony (GLME: $\chi^2$=2.38, $P$=0.123). A significant increase in the daily home range size as a function of time was found only for P31, for which the GPS recording period was the longest (35 days), but the effect was quite weak (linear regression: $F_{1,35}$=14.84, adjusted $R^2$=0.28, $P$=0.005).

## DISCUSSION

In a previous study, we reported that several acoustic features such as the fundamental frequency value, the call duration, the distribution of energy among the spectrum and the frequency modulation were individual-specific features in Cape fur seal mother and pup vocalisations (Martin et al., 2021b). Based on this study, we aimed to assess which acoustic features were effectively used in the process of decoding individual identity. We also intended to understand how the acoustic features of these affiliative calls are adapted to the Cape fur seal breeding system and allow mothers and pups to reunite after separation in a highly confusing environment. To this end, we studied the propagation properties of these vocalisations in the colony in relation to the size of the spatial range occupied by the pups in the absence of their mother.

First, playback experiments using artificially modified signals were performed to identify the acoustic features used in the cognitive process of decoding individual signatures. Based on previous knowledge of colonial or group-living mammals and birds, a combination of parameters in both the time and frequency domains of the call were varied and tested (Aubin and Jouventin, 2002; Charrier et al., 2001, 2002, 2003b, 2009; Pitcher et al., 2012; Sèbe et al., 2011).

Our study demonstrates that both mothers and pups use a multi-parameter vocal signature. They rely on frequency and/or amplitude

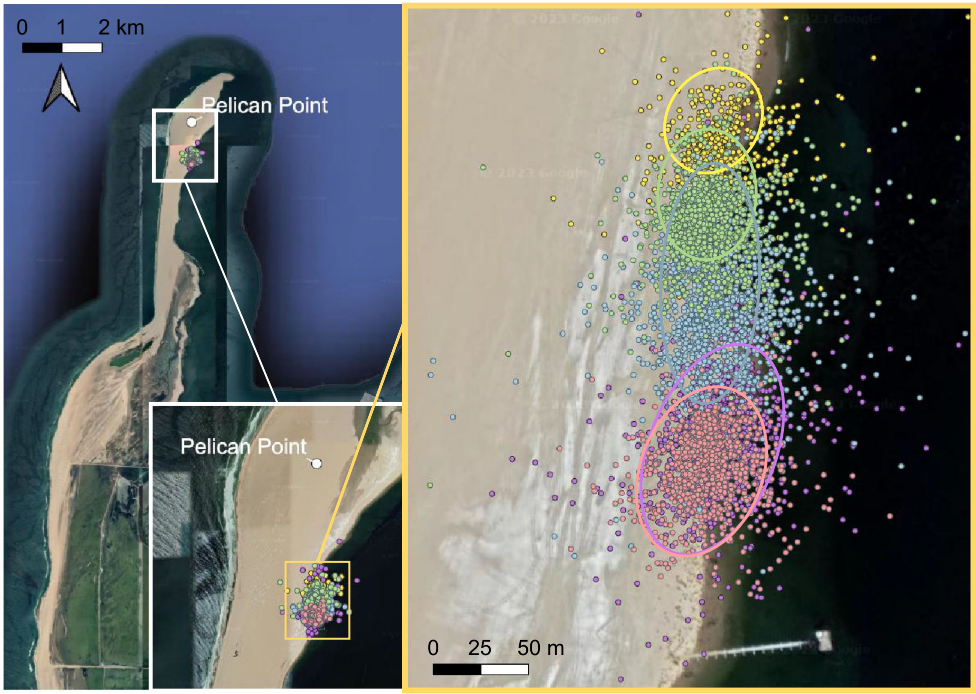

**Fig. 5. Map showing the positions recorded by the GPS tag of five pups during their entire recording period at Pelican Point, as well as the ellipse representing their overall home range of this period.** Only 5 of the 14 pups are shown for better readability, and these were chosen to limit data overlap.

modulations (FM/AM), on the amplitude spectrum (i.e. timbre) as well as the exact fundamental frequency values (i.e. perceptual voice pitch). Slight modifications in the fundamental frequency value (of 10 Hz for female and 20 Hz for pup vocalisations) did not affect recognition by the tested mothers and pups compared with the control series. As these slight shifts in the fundamental frequency were within the natural intra-individual variation in Cape fur seal PACs and FACs, these results were expected. Testing individuals may not be able to discriminate subtly different calls with weak variation in fundamental frequency (20 Hz or less) or, although detected, there may be a tolerance to these variations allowing vocal recognition despite a slight variation in the vocalisations produced. However, a frequency shift of 50 Hz strongly impaired the individual recognition in both mothers and pups.

In line with other pinniped species for which mutual mother–pup vocal recognition has been investigated such as in the subantarctic fur seal (Charrier et al., 2002, 2003a) and the Australian sea lion (Charrier et al., 2009; Pitcher et al., 2012), our findings on Cape fur seals show similar individual vocal signatures between mothers and pups. This suggests that, even at the age of a few days or more, pups have sufficient cognitive abilities to discriminate their mother's calls from other females' calls, and thus perceive subtle call variations in both time and frequency domains. In the present study, some pups were tested at less than 6 days of age (six individuals) and thus were still in the perinatal period (i.e. before the mother's first departure at sea). This suggests that the decoding of the maternal vocal signature is more likely to be the result of a fast learning process (that may start *in utero*) rather than a progressive development during the first months of the pup's life. Pups have been shown to recognise maternal calls as early as 4–6 h after birth (Martin et al., 2022a); therefore, it appears that the extreme colonial life of this species acts as a strong selection pressure on the recognition abilities of pups in the mother–pup vocal recognition system. In contrast to some pinniped species with lower social constraints, Cape fur seal pups appear to play an active role in reunion processes with their mother (Charrier, 2021). The early absences of females, lack of allo-nursing and aggressive behaviour of females towards non-filial pups are suggested to be important factors in shaping pups' vocal recognition abilities, as failed recognition and unsuccessful reunions represent a significant cost to the pup's survival (Insley, 2001).

Playback experiments conducted on pups revealed a high variability in their response to signals in which either the AM or the FM pattern was removed. Although their reaction to these series was significantly lower than their response to the control (Fig. 2), almost half of the pups displayed a vocal response to their broadcast and thus recognised their mother's vocalisations (whereas only 25% vocally responded to stranger, +50 Hz and ModSpectr; Fig. 3). These inter-individual variations in the decoding of the individual vocal signature are likely explained by the natural acoustic characteristics of a female's calls, and thus these will influence the parameters used by her pup to recognise her voice. For instance, in cases where a female produces calls with naturally weak FM (i.e. 'flat' calls), the removal of the FM is no longer a striking change for the pup, which will still recognise its mother's voice. In the same vein, we might ask whether the fact that females do not use AM (as pups do) is due to the characteristics of the pup' calls themselves. Indeed, owing to variation in the pups' emotional state (related to hunger, length of the mother's absence, possible physical aggression from other females), the AM in pups' vocalisations is likely to be unstable over time (Briefer, 2020). High intra-individual variation in this parameter could thus make it unreliable for individual recognition. Further studies would be interesting to assess how the natural structure of a call impacts its recognition by a conspecific. This could also have implications for its propagation in the environment and the quality of transmission of individual information in such an environment. Perhaps these physical (propagation) and cognitive (recognition) mechanisms act as selective pressures for certain parameters in the vocalisations of mothers and pups by playing a role in their ability to reunite in dense colonies. The use of other acoustic parameters (such as the initial part of the call or the slope of the fundamental frequency at the start of the call) in the decoding of the vocal individual signature has not been evaluated. Owing to field constraints and limitations on individuals' responsiveness (maintain motivation to respond to playbacks and avoiding habituation), we chose to limit the number of experimental signals tested in this study. Further investigations of the FM slope would be interesting in order to assess the accuracy in analysing such a feature by building signals with different modifications of the FM slope.

For all bird and mammal species in which the individual vocal signature has been experimentally investigated, the decoding process always involved the use of a combination of several acoustic features (Aubin and Jouventin, 2002; Aubin et al., 2015; Charrier et al., 2001, 2002, 2003a, 2009; Curé et al., 2016; Pitcher et al., 2012; Sèbe et al., 2011). This is most certainly a way to secure the individual identity code by maintaining vocal recognition in the case of a parameter being unreliable (e.g. degraded over the course of signal propagation) (Charrier, 2021). However, the Cape fur seal seems to use the largest number of parameters in combination. Indeed, among the four types of parameters that are generally studied (FM, AM, timbre and fundamental frequency), previous studies report the use of a maximum of two or three parameters. For instance, in the subantarctic fur seal, mothers and pups use the energy distribution of the call (pups seem to be more sensitive than females) and FM, whereas they do not rely on AM (Charrier et al., 2002, 2003a). In Antarctic fur seal, pups used AM, FM and the timbre (Aubin et al., 2015). In the Australian sea lion, both mothers and pups use AM and the pitch ($f_0$), but they still recognise their vocalisations when the spectrum is modified (Charrier et al., 2009; Pitcher et al., 2012). In addition, pups rely on FM while their mothers do not. Comparisons within colonial birds (Aubin and Jouventin, 2002) and other pinniped species (Charrier, 2021) showed that variations in the type of acoustic features and their combination for decoding the parent–young vocal signature are likely related to the selective pressures species face for individual recognition. As Cape fur seal breeding colonies are one of the largest among mammals, our present findings are consistent with this idea. Owing to this extreme density of individuals, the propagation of sound signals is constrained by seal bodies, which act as physical barriers. In addition, there is a masking effect owing to the loud background noise produced by the colony itself, i.e. seals vocalising. For these reasons, the use of a sophisticated vocal signature is likely to be advantageous for mother–pup pairs in ensuring an efficient and reliable transfer of information. For the other highly colonial pinniped species such as subantarctic and Antarctic fur seals, their colonial life also imposes a reliable coding–decoding system, but the lower density of colonies and lower colony size could act as lower selective pressures compared with the constraints faced by Cape fur seals. We suggest that the combined use of AM, FM, timbre and pitch would counteract the various degradations experienced by the signal during its propagation and increase the discriminability of signals in the background noise. Moreover, such combination of several acoustic features increases the coding possibilities, and thus the number of vocal signatures. Although the coding options are not infinite because the values of certain acoustic parameters are limited by anatomical constraints, the use of features such as the amplitude spectrum, AM or FM are a good way of increasing the number of possible combinations and therefore the level of vocal stereotypy between individuals. Moreover, the use of FM pattern analysis is known to be particularly effective in noisy environments, as signals with FM are more easily received and extracted (Lee and Jaynes, 1961; Okanoya and Dooling, 1991). Although slow AMs undergo degradation and distortion during transmission through a noisy environment (Wiley and Richards, 1978), this could have a short-range use for vocal identification. Fast AM (as shown in some females and bleating in pups' calls; Martin et al., 2021a,b) would help for distance estimation or for sound source localisation (Aubin et al., 2015).

Based on propagation tests performed on three different PACs and FACs, we assessed that their theoretical maximum propagation distance without significant degradation is 8 m in a quiet area (200 m distant from the seal colony). For females' calls, both the spectrogram and the amplitude spectrum had high correlation coefficients at 8 m, indicating that frequency values and FM are reliably propagated at this distance. In contrast, the poor reliability of the amplitude envelope points a very low transmission of AM, even at 8 m. These results show that the vocalisations of female Cape fur seals are subject to the general rules of degradation mentioned above, with a very low propagation of AM (Wiley and Richards, 1978).

For the FACs produced by pups (with or without bleating), only the spectrograms had correlation coefficients greater than 0.5 at 8 m (Fig. 4), indicating that pups' calls underwent more degradations than mothers' calls. Such a difference could be explained by the difference in acoustic structure and frequency content. Indeed, mothers' calls show more energy in lower frequencies compared with those of the pups. As high frequencies are more sensitive to degradation during propagation (Forrest, 1994; Hardt and Benedict, 2021), this could explain our results.

For all call types, signal reliability collapsed between 8 and 16 m (Fig. 4) and no correlation could be performed beyond 32 m as the signals were undetectable and totally confounded into the colony background noise. Our findings revealed that, at Pelican Point, a reliable vocal identification can only be performed within 8 m in a quiet area. We suggest that within the seal colony, this distance might be shorter because of the higher background noise and body effect masking (Aubin and Jouventin, 1998). However, Cape fur seal mothers and pups regularly experience separations at greater distances than 8 m. Indeed, based on data from GPS tracking, pups were reported to move into an area of approximately 60 m in radius around a point seen as the centre of their home range. Theoretically, the degradation of calls induced by their propagation properties and the background noise on the colony should prevent long-distance communication and thus complicate mother–young vocal recognition when the female is coming back to the shore. The exact same situation was highlighted for king penguin colonies, facing the same constraints of high background noise. King penguin calls do not propagate reliably beyond 7 m, but experiments reported that chicks are able to perceive and extract their parents' vocalisations from the ambient noise and that their recognition range is thus much greater than the theoretical propagation range estimated (11 versus 7 m) (Aubin and Jouventin, 1998). Known as the 'cocktail-party effect', it allows chicks to recognise parental calls at 6 dB below the level of background noise (Aubin and Jouventin, 1998). Given that Cape fur seal mothers and pups effectively reunite after a separation (and relatively quickly according to observations of marked individuals), we believe that similar abilities in extracting the sound from the noise could occur in this species to facilitate reunions. Although aerial hearing abilities were found to be quite similar among pinniped species (75 Hz to 30 kHz; see Erbe et al., 2016 for review), nothing is known about the masking effect of noise on aerial hearing abilities. Further studies are thus needed to investigate the abilities of pinnipeds to detect sounds at different distances in their natural environment, and their abilities to extract a signal from the noise. Depending on their social structure (from solitary to highly colonial species), differences in signal/noise extraction abilities among pinniped species are expected, as found among penguin species (Aubin and Jouventin, 2002). Furthermore, the redundancy associated with the repetition of calls produced by females and pups when searching for each other is surely an additional way of improving the efficiency of information transmission throughout the environment (Shannon and Weaver, 1949).

By tagging pups with a GPS logger for a minimum duration of 6 days, we described the position and size of their home range per day. Pup movements were reported to extend to a maximum of 60 m around a central point within a day, with a tag accuracy estimated at 18 m. Daily home ranges had a relatively stable position because they were separated by an average of 15 m between two consecutive days. In addition, almost all of them were located within the overall home range calculated over the whole recording period of a pup (with an average size of 66 m in radius). In the Cape fur seal, seal colony density is a factor that can limit the movement of individuals on the colony, especially for pups that are at risk of injury when they are too close to potentially aggressive adult females. The restriction of pup movements to a limited and spatially constant area is likely to reduce the search effort and associated energetic costs, especially in such dense colonies. Moreover, as reported in other otariid species, females likely use spatial cues to relocate their pup when returning to the colony after a foraging trip, and either go to the centre of their pup's home range or to the last suckling spot (Antarctic fur seal, Lunn and Boyd, 1991, Dobson and Jouventin, 2003; South American fur seal, *Arctocephalus australis*, Phillips, 2003; Galapagos sea lion, *Zalophus wollebaeki*, Wolf et al., 2007; Australian sea lion, Charrier et al., 2009). The spatial stability of the pup's living area over time is therefore crucial for mother and pup reunions. Contrary to expectations, we did not detect any link between the size of the home range (i.e. the size of the pup's exploration area) and the maternal attendance pattern. Indeed, in the Galapagos fur seal, *Arctocephalus galapagoensis*, pups were reported to spend less time playing and walking while with their mothers, owing to the long suckling sessions (Arnold and Trillmich, 1985). However, our observations of presence/absence of the mothers were performed only once or twice a day and therefore we might have missed the presence/absence of the mother. Indeed, if a mother was seen in the morning, she could have gone to sea a few moments later and left her pup alone for the day. For this reason, our analysis may have underestimated or overestimated the presence of the female with her pup, depending on the situation. In addition, most tagged pups were possibly too young (less than 2 months old) to show advanced exploratory behaviour. Pup P14 was the only pup that showed a significant increase in the distance travelled per day after several days of absence of its mother, suggesting that starvation may induce more active searching behaviours. For the pup whose movements were recorded over the longest period (P31, 35 days), we found a slight increase in the size of the home range over time. This suggests a broadening of the pups' exploratory abilities with age but remains to be verified with additional long-term deployments of GPS tags (e.g. over the entire lactation period or at least until moulting). The other pups tagged in this study probably had recording times too short to detect such variations. In other species, such as the Antarctic fur seal, pup exploration movements were not related to intrinsic factors such as age or body size, or to extrinsic factors such as ambient temperature (Nagel et al., 2021).

## Conclusions

To conclude, four acoustic features in both time and frequency domains were found to be involved in the Cape fur seal mother–pup individual identification process: AM, FM, timbre and pitch. The use of such a high number of acoustic features has never been shown before in a colonial species. This could be explained by a significant effect of the environmental and social constraints faced by this extremely colonial species. Propagation tests showed that the calls produced by mothers and pups are degraded at very short distances (8 m or less), below the distance at which they are usually separated (approximately 60 m). We suggest that long-distance communication allowing mother–pup reunions after a foraging trip is likely enabled by the strong abilities of individuals to extract signal properties from ambient noise, known as the 'cocktail-party effect'.

### Acknowledgements

We acknowledge the support of the Namibian Ministry of Fisheries and Marine Resources and the Namibian Chamber of Environment for this research.

### Competing interests

The authors declare no competing or financial interests.

### Author contributions

Conceptualization: M.M., I.C.; Formal analysis: M.M.; Data curation: M.M., A.I., I.C.; Writing - original draft: M.M.; Writing - review & editing: T.G., A.I., S.E., I.C.; Visualization: M.M.; Supervision: T.G., I.C.; Project administration: T.G., S.E.; Funding acquisition: I.C.

### Funding

This project has received financial support from the Centre National de la Recherche Scientifique (CNRS, France) through the MITI interdisciplinary programs.

### Data availability

Raw data are available from the Zenodo repository: doi:10.5281/zenodo.8116997

### References

**Arnold, W. and Trillmich, F.** (1985). Time budget in Galapagos fur seal pups: the influence of the mother's presence and absence on pup activity and play. *Behaviour* **92**, 302-321.

**Aubin, T. and Jouventin, P.** (1998). Cocktail-party effect in king penguin colonies. *Proc. R. Soc. B Biol. Sci.* **265**, 1665-1673. doi:10.1098/rspb.1998.0486

**Aubin, T. and Jouventin, P.** (2002). How to vocally identify kin in a crowd: the penguin model. *Adv. Study Behav.* **31**, 243-277. doi:10.1016/S0065-3454(02)80010-9

**Aubin, T., Jouventin, P. and Charrier, I.** (2015). Mother vocal recognition in Antarctic fur seal *Arctocephalus gazella* pups: a two-step process. *PLoS One* **10**, e0134513. doi:10.1371/journal.pone.0134513

**Bartosova-Vichova, J., Bartoš, L. and Švecová, L.** (2007). Technical note: preorbital gland opening in red deer (*Cervus elaphus*) calves as an indicator of stress. *J. Anim. Sci.* **85**, 494-496. doi:10.2527/jas.2006-446

**Bates, D., Maechler, M., Bolker, B. and Walker, S.** (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1-48. doi:10.18637/jss.v067.i01

**Blumstein, D. T. and Munos, O.** (2005). Individual, age and sex-specific information is contained in yellow-bellied marmot alarm calls. *Anim. Behav.* **69**, 353-361. doi:10.1016/j.anbehav.2004.10.001

**Briefer, E. F.** (2020). Coding for 'dynamic' information: vocal expression of emotional arousal and valence in non-human animals. In *Coding Strategies in Vertebrate Acoustic Communication* (ed. T. Aubin and N. Mathevon), pp. 137-162. Cham: Springer.

**Carlson, N. V., Kelly, E. M. K. and Couzin, I.** (2020). Individual vocal recognition across taxa: a review of the literature and a look into the future: individual vocal recognition. *Philos. Trans. R. Soc. B Biol. Sci.* **375**, 20190479. doi:10.1098/rstb.2019.0479

**Charrier, I.** (2021). Vocal communication in otariids and odobenids. In *Ethology and Behavioral Ecology of Otariids and the Odobenid* (ed. C. Campagna and R. G. Harcourt), pp. 265-289. Springer, Cham.

**Charrier, I., Mathevon, N., Jouventin, P. and Aubin, T.** (2001). Acoustic communication in a black-headed gull colony: how do chicks identify their parents? *Ethology* **107**, 961-974. doi:10.1046/j.1439-0310.2001.00748.x

**Charrier, I., Mathevon, N. and 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. doi:10.1242/jeb.205.5.603

**Charrier, I., Mathevon, N. and Jouventin, P.** (2003a). Vocal signature recognition of mothers by fur seal pups. *Anim. Behav.* **65**, 543-550. doi:10.1006/anbe.2003.2073

**Charrier, I., Mathevon, N. and Jouventin, P.** (2003b). Fur seal mothers memorize subsequent versions of developing pups' calls: adaptation to long-term recognition or evolutionary by-product? *Biol. J. Linn. Soc.* **80**, 305-312. doi:10.1046/j.1095-8312.2003.00239.x

**Charrier, I., Pitcher, B. J. and Harcourt, R. G.** (2009). Vocal recognition of mothers by Australian sea lion pups: individual signature and environmental constraints. *Anim. Behav.* **78**, 1127-1134. doi:10.1016/j.anbehav.2009.07.032

**Curé, C., Mathevon, N. and Aubin, T.** (2016). Mate vocal recognition in the Scopoli's shearwater *Calonectris diomedea*: do females and males share the same acoustic code? *Behav. Processes* **128**, 96-102. doi:10.1016/j.beproc.2016.04.013

**David, J. H. M. and Rand, R. W.** (1986). Attendance behavior of South African fur seals. In *Fur Seals: Maternal Strategies on Land and at Sea* (ed. R. L. Gentry and G. L. Kooyman), pp. 126-141. Princeton: Princeton University Press.

**Déaux, É. C., Charrier, I. and Clarke, J. A.** (2016). The bark, the howl and the bark-howl: identity cues in dingoes' multicomponent calls. *Behav. Processes* **129**, 94-100. doi:10.1016/j.beproc.2016.06.012

**Deecke, V. B.** (2006). Studying marine mammal cognition in the wild: a review of four decades of playback experiments. *Aquat. Mamm.* **32**, 461-482. doi:10.1578/AM.32.4.2006.461

**Dentressangle, F., Aubin, T. and Mathevon, N.** (2012). Males use time whereas females prefer harmony: individual call recognition in the dimorphic blue-footed booby. *Anim. Behav.* **84**, 413-420. doi:10.1016/j.anbehav.2012.05.012

**Dobson, F. S. and Jouventin, P.** (2003). How mothers find their pups in a colony of Antarctic fur seals. *Behav. Processes* **61**, 77-85. doi:10.1016/S0376-6357(02)00164-X

**Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K. and Dooling, R.** (2016). Communication masking in marine mammals: a review and research strategy. *Mar. Pollut. Bull.* **103**, 15-38. doi:10.1016/j.marpolbul.2015.12.007

**Forrest, T. G.** (1994). From sender to receiver: propagation and environmental effects on acoustic signals. *Integr Comp Biol* **34**, 644-654. doi:10.1093/icb/34.6.644

**Fox, J. and Weisberg, S.** (2019). *An R Companion to Applied Regression*, 3rd edn. Thousand Oaks, CA: Sage.

**Friard, O. and Gamba, M.** (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol. Evol.* **7**, 1325-1330. doi:10.1111/2041-210X.12584

**Gamel, C. M., Davis, R. W., David, J. H. M., Meÿer, M. A. and Brandon, E.** (2005). Reproductive energetics and female attendance patterns of Cape fur seals (*Arctocephalus pusillus pusillus*) during early lactation. *Am. Midl. Nat.* **153**, 152-170. doi:10.1674/0003-0031(2005)153[0152:REAFAP]2.0.CO;2

**Halliday, T. R. and Slater, P. J. B.** (1983). *Animal Behaviour, Vol. 2. Communication*. Oxford: Blackwell Scientific Publications.

**Harcourt, R.** (1992). Maternal aggression in the South American fur seal in Peru. *Can. J. Zool.* **70**, 320-325. doi:10.1139/z92-048

**Hardt, B. and Benedict, L.** (2021). Can you hear me now? A review of signal transmission and experimental evidence for the acoustic adaptation hypothesis. *Bioacoustics* **30**, 716-742. doi:10.1080/09524622.2020.1858448

**Insley, S. J.** (2001). Mother–offspring vocal recognition in northern fur seals is mutual but asymmetrical. *Anim. Behav.* **61**, 129-137. doi:10.1006/anbe.2000.1569

**Lee, Y. W. and Jaynes, E. T.** (1961). Statistical theory of communication. *Am. J. Phys.* **29**, 276-278. doi:10.1119/1.1937745

**Lunn, N. J. and Boyd, I. L.** (1991). Pupping-site fidelity of Antarctic fur seals at Bird Island, South Georgia. *J. Mammal.* **72**, 202-206. doi:10.2307/1381999

**Manser, M. B., Madden, J. R., Kunc, H. P., English, S. and Clutton-Brock, T.** (2008). Signals of need in a cooperatively breeding mammal with mobile offspring. *Anim. Behav.* **76**, 1805-1813. doi:10.1016/j.anbehav.2008.07.027

**Martin, M., Gridley, T., Elwen, S. and Charrier, I.** (2021a). Vocal repertoire, micro-geographical variation and within-species acoustic partitioning in a highly colonial pinniped, the Cape fur seal. *R. Soc. Open Sci.* **8**, 1-18. doi:10.1098/rsos.202241

**Martin, M., Gridley, T., Elwen, S. and Charrier, I.** (2021b). Extreme ecological constraints lead to high degree of individual stereotypy in the vocal repertoire of the Cape fur seal (*Arctocephalus pusillus pusillus*). *Behav. Ecol. Sociobiol.* **75**, 1-16. doi:10.1007/s00265-020-02935-9

**Martin, M., Gridley, T., Elwen, S. and Charrier, I.** (2022a). Early onset of postnatal individual vocal recognition in a highly colonial mammal species. *Proc. R. Soc. B Biol. Sci.* **289**, 20221769. doi:10.1098/rspb.2022.1769

**Martin, M., Gridley, T., Fourie, D., Elwen, S. H. and Charrier, I.** (2022b). Mutual mother–pup vocal recognition in the highly colonial Cape fur seal: evidence of discrimination of calls with a high acoustic similarity. *Anim. Cogn* **25**, 1461-1472. doi:10.1007/s10071-022-01627-3

**Matrosova, V. A., Blumstein, D. T., Volodin, I. A. and Volodina, E. V.** (2011). The potential to encode sex, age, and individual identity in the alarm calls of three species of Marmotinae. *Naturwissenschaften* **98**, 181-192. doi:10.1007/s00114-010-0757-9

**McCulloch, S., Pomeroy, P. P. and Slater, P. J. B.** (1999). Individually distinctive pup vocalizations fail to prevent allo-suckling in grey seals. *Can. J. Zool.* **77**, 716-723. doi:10.1139/z99-023

**McGregor, P. K.** (1992). Quantifying responses to playback: one, many, or composite multivariate measures? In *Playback and Studies of Animal Communication* (ed. D. M. Power), pp. 79-96. New York: Springer.

**Nagel, R., Mews, S., Adam, T., Stainfield, C., Fox-Clarke, C., Toscani, C., Langrock, R., Forcada, J. and Hoffman, J. I.** (2021). Movement patterns and activity levels are shaped by the neonatal environment in Antarctic fur seal pups. *Sci. Rep.* **11**, 1-12. doi:10.1038/s41598-021-93253-1

**Okanoya, K. and Dooling, R. J.** (1991). Detection of species-specific calls in noise by zebra finches *Poephila guttata* and budgerigars *Melopsittacus undulatus*: time of frequency domain? *Bioacoustics* **3**, 163-172. doi:10.1080/09524622.1991.9753177

**Phillips, A. V.** (2003). Behavioral cues used in reunions between mother and pup south American fur seals (*Arctocephalus australis*). *J. Mammal.* **84**, 524-535. doi:10.1644/1545-1542(2003)084<0524:BCUIRB>2.0.CO;2

**Pitcher, B. J., Harcourt, R. G. and Charrier, I.** (2012). Individual identity encoding and environmental constraints in vocal recognition of pups by Australian sea lion mothers. *Anim. Behav.* **83**, 681-690. doi:10.1016/j.anbehav.2011.12.012

**Rand, R. W.** (1955). Reproduction in the female Cape Fur Seal, *Arctocephalus pusillus* (Schreber). *Proc. Zool. Soc. London* **124**, 717-740. doi:10.1111/j.1469-7998.1955.tb07812.x

**Rand, R. W.** (1967). The Cape fur seal *Arctocephalus pusillus pusillus* 3. General behaviour on land and at sea. *Sea Fish. Inst. Investg. Rep* **60**, 1-32.

**Riedman, M.** (1990). *The Pinnipeds: Seals, Sea Lions, and Walruses*. Vol. 12. University of California Press.

**Searby, A. and Jouventin, P.** (2003). Mother-lamb acoustic recognition in sheep: a frequency coding. *Proc. R. Soc. B Biol. Sci.* **270**, 1765-1771. doi:10.1098/rspb.2003.2442

**Sèbe, F., Aubin, T., Nowak, R., Sèbe, O., Perrin, G. and Poindron, P.** (2011). How and when do lambs recognize the bleats of their mothers? *Bioacoustics* **20**, 341-355. doi:10.1080/09524622.2011.9753656

**Shannon, C. E. and Weaver, W.** (1949). *The Mathematical Model of Communication*. Urbana, IL: University of Illinois Press.

**Sherman, P. W., Reeve, H. and Pfennig, D.** (1997). Recognition systems. In *Behavioural Ecology: An Evolutionary Approach* (ed. J. R. Krebs and N. B. Davies), pp. 69-96. Blackwell Science Limited.

**Sousa-Lima, R. S., Paglia, A. P. and Da Fonseca, G. A. B.** (2002). Signature information and individual recognition in the isolation calls of Amazonian manatees, *Trichechus inunguis* (Mammalia: Sirenia). *Anim. Behav.* **63**, 301-310. doi:10.1006/anbe.2001.1873

**Sueur, J., Aubin, T. and Simonis, C.** (2008). Seewave, a free modular tool for sound analysis and synthesis. *Bioacoustics* **18**, 213-226. doi:10.1080/09524622.2008.9753600

**Townsend, S. W., Hollén, L. I. and Manser, M. B.** (2010). Meerkat close calls encode group-specific signatures, but receivers fail to discriminate. *Anim. Behav.* **80**, 133-138. doi:10.1016/j.anbehav.2010.04.010

**Tripovich, J. S., Canfield, R., Rogers, T. L. and Arnould, J. P. Y.** (2009). Individual variation of the female attraction call produced by Australian fur seal pups throughout the maternal dependence period. *Bioacoustics* **18**, 259-276. doi:10.1080/09524622.2009.9753605

**Trivers, R. L.** (1974). Parent-offspring conflict. *Am. Zool.* **14**, 249-264. doi:10.1093/icb/14.1.249

**Wiley, R. H. and Richards, D. G.** (1978). Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* **3**, 69-94. doi:10.1007/BF00300047

**Wolf, J. B. W., Mawdsley, D., Trillmich, F. and James, R.** (2007). Social structure in a colonial mammal: unravelling hidden structural layers and their foundations by network analysis. *Anim. Behav.* **74**, 1293-1302. doi:10.1016/j.anbehav.2007.02.024

**Wyman, M. T., Walkenhorst, B. and Manser, M. B.** (2022). Selection levels on vocal individuality: strategic use or. *Curr. Opin. Behav. Sci.* **46**, 101140. doi:10.1016/j.cobeha.2022.101140