

In-air acoustic repertoire and associated behaviour of wild juvenile crabeater seals during rehabilitation

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Abstract

In-air sounds of pinnipeds are important for interactions with conspecifics and threat displays. However, little is known about the in-air acoustic repertoire and associated behaviour of crabeater seals *Lobodon carcinophaga*. We investigated the in-air acoustic repertoire and associated behaviour of two male and one female wild juvenile crabeater seals that beached separately, and were rehabilitated in Durban and Gqeberha, South Africa. In-air sounds were visually identified and categorised into five classes validated via random forest model classification: brief, intermediate and long moan calls, croaks, and hisses. Hisses were common (n= 25,105 sounds from 136 hours of acoustic recordings) and detected during heightened arousal states and interactions with animal care staff and a conspecific. Furthermore, hisses were also recorded in low arousal states during exhalation. Moan calls (n= 241) were only detected from two of the three seals. During rehabilitation, the female seal ceased producing moan calls and later produced a series of croaks (n= 204). Acoustic characteristics of in-air moan calls differed from published underwater moan calls according to duration, minimum and maximum frequencies, and pulse repetition rate. Our study shows that the in-air acoustic repertoire and associated behaviour of these Antarctic seals are dynamic, vary inter-individually and are context dependent.

Keywords: Acoustic behaviour, *Lobodon carcinophaga*, Antarctic pinnipeds, acoustic repertoire, in-air sounds, South Africa

Introduction

Pinnipeds are vocally active animals with a diverse acoustic repertoire that can be divided into sounds made in-air and underwater (e.g., Stirling and Siniff 1979; Watkins and Ray 1985; Terhune et al. 1994; Collins et al. 2011). In-air vocalisations are well studied in some species; for example, at least eight in-air call types exist for Weddell seals *Leptonychotes weddellii* during the breeding season (Terhune et al. 1994; Collins and Terhune 2007). Some of those in-air calls are also produced underwater and vary seasonally and geographically (e.g., Stirling and Siniff 1979; Thomas et al. 1988; Morrice et al. 1994; Rogers et al. 1996). Pinnipeds use in-air sounds for male–male

competition, attracting females, mother-pup communication, aggression displays to conspecifics and other perceived threats, and for inter-species interactions (Nel 1966; Sanvito and Galimberti 2000; Insley et al. 2003; Rogers 2003; Sanvito et al. 2007). Contact calling is common between mother and pups, and aerial exchanges of pup attraction calls and female attraction calls are well documented in gregarious otariid seals such as Antarctic fur seal *Arctocephalus gazella* (e.g., Aubin et al. 2015) and sub-Antarctic fur seal *Arctocephalus tropicalis* (Charrier et al. 2002, 2003). Identity information is encoded within the acoustic cues of these in-air vocalizations, facilitating mother-pup vocal recognition at high-density breeding colonies (Charrier et al. 2003; Insley et al. 2003). However, mother-pup acoustic communication is less pronounced in phocid seals. Mother-pup recognition in phocids is mainly based instead on a combination of sensory modalities such as olfactory and spatial cues (Terhune et al. 1979; Kovacs et al. 1995; Insley et al. 2003).

Despite being the most abundant seal species in the world (Southwell et al. 2012) and possibly the most abundant large mammal (Hückstädt 2015), the acoustic ecology of crabeater seals *Lobodon carcinophaga* is less studied compared to other less abundant Antarctic phocids such as the Ross seal *Ommatophoca rossii* (e.g., Watkins and Ray 1985; Shabangu and Rogers 2021), and the Weddell seal (e.g., Terhune et al. 1994; Terhune and Dell'Apa 2006; Collins and Terhune 2007; Collins et al. 2011). With a circumpolar Antarctic distribution, crabeater seals inhabit the pack ice zone year-round, making it logistically difficult to survey them at certain times of the year as those habitats are at times inaccessible (e.g., Bengtson 2009; Bengtson et al. 2011). Consequently, information on the acoustic repertoire and acoustic behaviour of crabeater seals is mostly limited to passive acoustic underwater recordings (e.g., Stirling and Siniff 1979; McCreery and Thomas 2009; Klinck et al. 2010; van Opzeeland et al. 2010; Shabangu

and Charif 2021; Nagaraj et al. 2021). The underwater acoustic repertoire of crabeater seals consist of short, low, and high moan calls, short groans, whistles, screeches, and grunts (Stirling and Siniff 1979; McCreery and Thomas 2009; Klinck et al. 2010; Shabangu and Charif 2021). These underwater recordings revealed a seasonal pattern in the detection of crabeater seal moan calls, which is indicative of seal presence and/or different behaviours (Stirling and Siniff 1979; McCreery and Thomas 2009; Klinck et al. 2010; van Opzeeland et al. 2010; Shabangu and Charif 2021; Nagaraj et al. 2021).

Groups of crabeater seals consisting of more than a thousand individuals are often found on the pack ice, the edge of the continental shelf and marginal ice zone, where most seals haul out during the day after foraging at sea overnight (Siniff et al. 1979; Burns et al. 2004; Southwell et al. 2005; Bengtson 2009). The high densities of these animals and social interactions between them at haul out sites may generate a selective pressure for a complex in-air acoustic communication system. However, to-date, there has been limited investigation into the in-air acoustic behaviour of crabeater seals (e.g., Nel 1966; Siniff et al. 1979). Previously documented in-air sounds of crabeater seals in Antarctica include bawls, growls, harsh barks, hisses, and snarls (Nel 1966; Cline et al. 1969; Siniff et al. 1979); however, these studies only provide aural descriptions of those sounds without providing any acoustic structural properties (frequency ranges and duration) or quantitative categorisation to distinguish sound types. Crabeater seals were earlier observed to produce hisses as part of an agonistic display when they were threatened by humans (Nel 1966), with observational descriptions suggesting the level of aggression being more intense in older seals than younger ones (Cline et al. 1969).

Crabeater seals feed primarily on Antarctic krill *Euphausia superba*, which comprises 95% of their diet, with fish and cephalopods contributing a small portion of their diet (Laws 1984; Forcada et al. 2012; Hückstädt et al. 2012). Their distribution is

therefore driven by the distribution and abundance of Antarctic krill (Nachtsheim et al. 2017; Hückstädt et al. 2020). Although sightings or strandings of these seals are rare outside of Antarctica, they have been reported for southern coasts of Africa, Australia and South America, and for New Zealand (Bengtson 2009; Hückstädt 2015), with thirty-three crabeater seals found on the South African coast since 1957 (Vinding et al. unpublished data). Of these, six were held for rehabilitation where two seals survived for three months each in 1973 and 1974 (Ross et al. 1975), while a third survived for six months in 1989 (Vinding et al. unpublished data). A further three stranded seals were captured for rehabilitation in 2021 and are the subject of this study.

Rehabilitation centres provide an opportunity to conduct behavioural research since animals can be studied in an easily accessible controlled environment (Jayne and See 2019). The objective of this study was to determine the in-air acoustic repertoire of three juvenile crabeater seals and describe their associated behaviour during rehabilitation. Furthermore, we aimed to compare the in-air acoustic repertoire to the underwater acoustic repertoire in published literature of this species.

Materials and Methods

Recording of seal sounds

This study focuses on two male and one female juvenile crabeater seals (Table 1). The males were stranded on the 28th of January 2021, one (hereafter Ragnar) in Ramsgate, 137 km south of Durban, and the other (hereafter Sebastian) outside of East London, 200 km east of Gqeberha (Table 1). The female seal (hereafter Pearl) stranded on the 07th May 2021 in Wilderness, 300 km west of Gqeberha (Table 1). Health assessment of all seals by local veterinarians indicated that they were healthy although underweight, and there were no signs of ailments or diseases that may have affected their acoustic

Table 1. Summary of focal crabeater seals with information on stranding and rehabilitation history in South Africa. * denotes part of the pen is displayed in Video A1.

Seal name	Sex	Date stranded	Stranded location (geographic coordinates)	Rehabilitation centre (city name; geographic coordinates)	Housing details	Housing partner	Release date (release location)	Dorsal standard length/weight on release
Ragnar	Male	28/01/2021	Ramsgate (30.86° S, 30.37° E)	uShaka Sea World (Durban; 29.87° S, 31.05° E), transferred to Bayworld (Gqeberha; 33.98° S, 25.65° E) on 18/02/2021	Enclosure: 89 m ² indoor area Pool area: 48.45 m ²	Housed from 12 to 18 February with yearling southern elephant seal <i>Mirounga leonina</i>	19/02/2021 (40 nm offshore of Cape Recife, approximately at 34.4° S, 26.0° E)	1.57 m/61 kg
Sebastian	Male	28/01/2021	East London (33.03° S, 27.86° E)	Bayworld (Gqeberha; 33.98° S, 25.65° E)	*Enclosure: 15 m ² outdoor pen area Pool area: 2.5 m ²	Housed from 28 January to 17 February in solitary and from 18 to 19 February with Ragnar	19/02/2021 (40 nm offshore of Cape Recife, approximately at 34.4° S, 26.0° E)	1.61 m/62 kg
Pearl	Female	07/05/2021	Wilderness (33.98° S, 22.58° E)	Bayworld (Gqeberha; 33.98° S, 25.65° E)	Same as Sebastian	Housed from 07 May to 23 August in solitary	23/08/2021 (40 nm offshore of Cape Recife, approximately at 34.4° S, 26.0° E)	1.81 m/120 kg

Table 2. Summary of in-air recording sessions for each recorder type used in Durban and Gqeberha.

Seal name(s)	Period (number of sampling days)	Recording device	Recording duration (hours)	Sampling rate	Frequency response	Regime	Behavioural observation in view of the seal(s)
Ragnar	16–18/02/2021 (3 days)	AudioMoth 1.2.0 within 10 m distance from the seal	2.45	96 kHz	100 Hz to 17 kHz	Dedicated	Yes, real time observer within 10 m from the seal
Sebastian	02–12/02/2021 (4 days)	Blackview BV4000 smartphone within 5 m distance from the seal	1.07	48 kHz	20 Hz to 20 kHz	Opportunistic	Yes, video data within 5 m from the seal
Sebastian & Ragnar	18/02/2021 (1 day)	Blackview BV5500 smartphone within 5 m distance from seals	0.25	48 kHz	20 Hz to 20 kHz	Dedicated	Yes, video data within 5 m from seals
	18/02/2021 (1 day)	Olympus VN-3500PC digital recorder with a handheld Sony F-V4T unidirectional microphone within 5 m distance from seals	2.39	44.1 kHz	90 Hz to 13 kHz	Dedicated	Yes, video data within 5 m from seals
Pearl	22/05–27/06/2021 (12 days)	AudioMoth 1.2.0 within 3 m distance from the seal	130.43	96 to 384 kHz	100 Hz to 17 kHz	Dedicated	Yes, real time observers within 5 m from the seal

behaviour. Their weights and lengths (Table 1) indicate that all three seals were likely under-yearlings born in the previous breeding season (September–December 2020) (Laws 1958; Shaughnessy and Kerry 1989; Laws et al. 2003; Shaughnessy et al. 2019). All seals were taught to feed on defrosted fish, initially with a meal in the evening, but later an additional meal in the morning. Sounds of all seals were recorded during rehabilitation, and the data collection periods and equipment type used, including sampling rates and recording duration, are summarised in Table 2. Additionally, underwater acoustic data were collected in Durban using a SoundTrap 300 STD recorder (Ocean Instruments NZ, New Zealand) with a sampling rate of 288 kHz that was deployed at a 1 m maximum depth for short periods of time during dedicated recording sessions over three days. Real time observer and video data (using a GoPro Hero 5) were collected within 10 m of the seal to supplement these underwater acoustic recordings.

Measurement of sound characteristics

In-air sounds of crabeater seals were visually and aurally reviewed in the spectrogram display (Figure 1) of Raven Pro version 1.6.1 (Center for Conversation Bioacoustics 2019). Spectrogram parameters of 50% overlap, discrete Fourier transform size: 16,384 samples, and 0.411 s Hann window were used for the visual review, and parameters in Figure 1 were used for zoomed in evaluation of sounds. Visually detected sounds were categorised into five descriptive groups: brief, intermediate and long moan calls, croaks, and hisses. Moan calls were categorised and counted according to spectral and duration characteristics of previously described underwater crabeater seal calls (Klinck et al. 2010; Shabangu and Charif 2021; Appendix A: Table A1). Spectral properties of the previously undescribed croaks and hisses were used to visually classify and count these

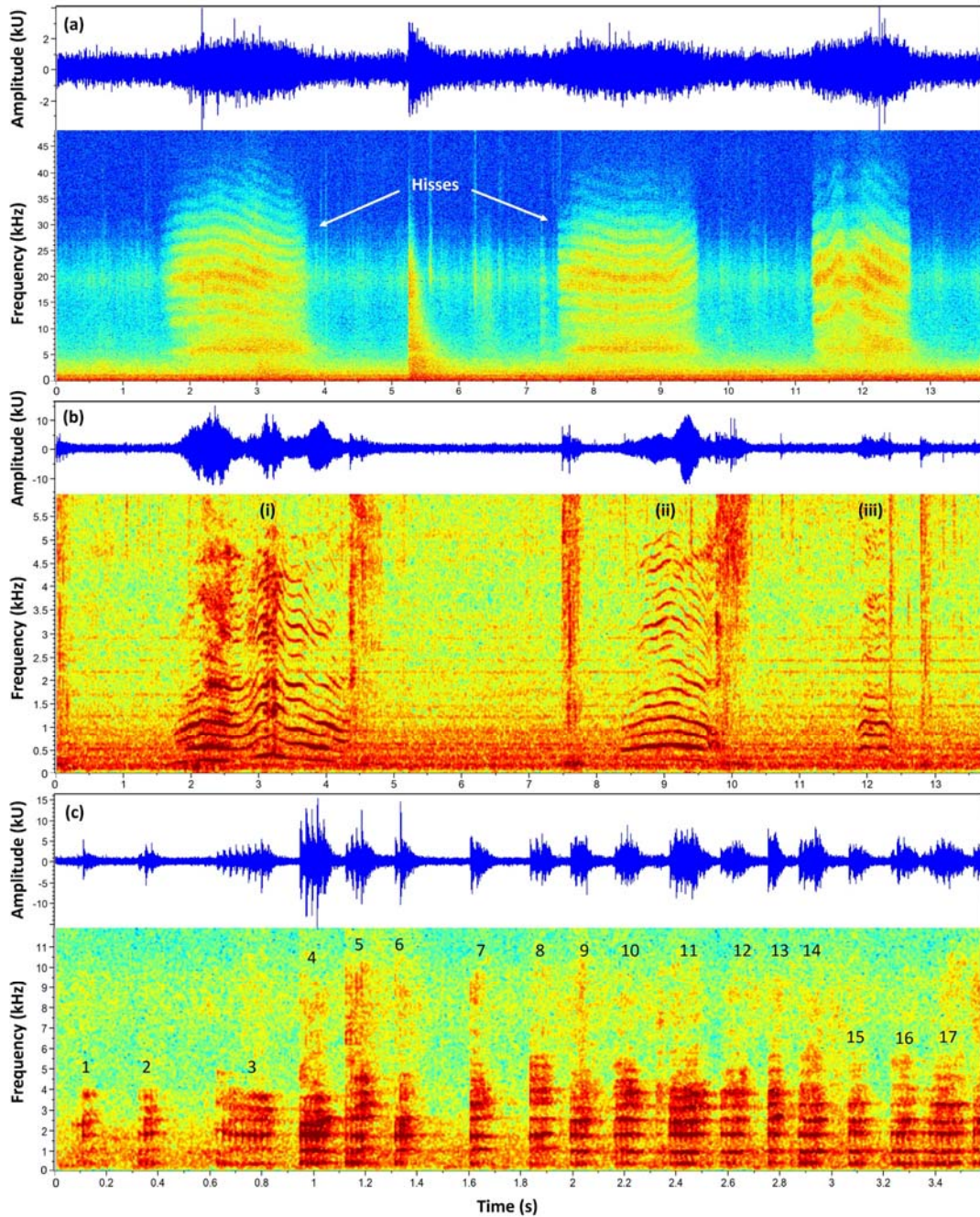


Figure 1. Amplitudes and spectrograms of juvenile crabeater seal (a) hisses recorded in Durban, (b) moan calls and (c) a series of 17 croaks (numbered sequentially) recorded in Gqeberha. Note differing x- and y-axes scales. kU is for kilo Unit. Three types of moan calls are shown in (b): (i) long moan call, (ii) intermediate moan call and (iii) brief moan call. Spectrogram parameters: (a) frame size 0.01 s, 50% overlap, discrete Fourier transform (DFT) size 2,048 samples, Hann window; (b) frame size 0.03 s, 50% overlap, DFT size 2,048 samples, Hann window; (c) frame size 0.02 s, 50% overlap, DFT size 2,048 samples, Hann window.

sounds. Croaks were termed so because of their auditory characteristics to human observers, and hisses were defined as strident sounds detected when air was exhaled through the seals' nostrils as confirmed through visual observation.

Following methods summarised in Shabangu and Charif (2021), we measured the minimum (0% and 5%), peak and maximum (95% and 100%) frequencies (Hz), 90% and 100% duration (s) and pulse repetition rate (PRR) of sound types with a signal-to-noise ratio (SNR) greater than 10 dB, where the waveform was free from clipping. The 100% maximum frequency was measured to the maximum ceiling frequency across the full spectrum of the sound including all true harmonics. Only acoustic data from Ragnar and Pearl collected using AudioMoth recorders were used to determine the acoustic characteristics of hisses (Sebastian's hisses were not measured due to limited sampling rate of recorders), as these recorders, sampling the environment above 96 kHz, captured the full frequency range of these sounds. Inter-series interval (ISI) and inter-hiss interval (IHI) were measured to determine the time delay between the end and start of a series of hisses, and between the end and start of individual hisses respectively. Series of hisses were characterised by clustered sounds occurring within a minute bout. Inter-call interval (ICI) of croaks were measured to indicate the time delay between the end and start of each croak within a series.

Characteristics of all in-air moan calls from Sebastian were measured from the acoustic data collected using a smartphone (Blackview B5500) and handheld microphone (Sony F-V4T), since the majority of high SNR (>10 dB) sounds were recorded using those instruments. Permutational multivariate analysis of variance (PERMANOVA) test (Appendix B) revealed no statistical difference in the key parameters (0% minimum frequency, 100% maximum frequency, 100% duration and

peak frequency) of moan calls and no interaction between call type and instrument type (Appendix B: Table B1). These data were therefore pooled in subsequent analysis. Acoustic data collected using the AudioMoth recorder were used to measure the characteristics of croak calls, as these were only recorded using that recorder type. Statistics summarising the acoustic characteristics of each sound type were calculated using the ‘pastecs’ package (Grosjean and Ibanez, 2018) in R (version 4.0.5; R Core Team 2021). We used Welch two-sample t-tests using the ‘DescTools’ package (Signorell et al. 2020) in R to test differences in acoustic characteristics between two recording sessions at a time. This test does not assume that the variance is the same between two groups.

To determine the comparability of characteristics (5% minimum frequency, peak frequency, 95% maximum frequency, 90% duration, and PRR) of in-air moan calls (produced by juveniles; this study) to previously published accounts of underwater moan calls (age unknown; Klinck et al. 2010; Shabangu and Charif 2021), Welch two sample t-tests were performed using the mean, standard deviation and sample size of each moan call type (Table 3; Appendix A: Table A1). The structure of pulses in a subsample of 20 intermediate moan call (being the most detected in-air moan call) waveforms was evaluated and compared to that of the underwater short moan call presented in Shabangu and Charif (2021).

Repertoire and classification of in-air sounds

To validate the accuracy of the above visual sound type categorizations and to determine important variables for classifying sounds, we fitted global multi-level classification random forest (RF) models (Breiman 2001) using the ‘randomForest’ package (Liaw and Wiener 2002) in R. Here measured acoustic characteristics were

Table 3. Statistics (average \pm standard deviation (range)) of the acoustic characteristics of recorded sounds of juvenile crabeater seals. n is the sample size of sounds, and – represents instances when characteristics were not measurable.

Sound name	Sound producing seal(s)	0% Minimum frequency (Hz)	5% Minimum frequency (Hz)	Peak frequency (Hz)	95% Maximum frequency (Hz)	100% Maximum frequency (Hz)	90% Duration (s)	100% Duration (s)	PRR (Hz)
Hiss (n=210)	Ragnar & Pearl	2,004 \pm 1,175 (0–5,357)	5,704 \pm 1,877 (1,758–15,094)	16,733 \pm 4,177 (1,805–22,898)	24,216 \pm 2,444 (19,969–31,711)	38,796 \pm 5,043 (29,106–46,880)	1.29 \pm 0.59 (0.19–4.75)	1.76 \pm 0.76 (0.33–6.16)	–
Long moan (n=11)	Sebastian	148 \pm 72 (65–312)	429 \pm 105 (258–517)	643 \pm 222 (345–1,120)	2,250 \pm 744 (1,077–3,047)	5,074 \pm 331 (4,460–5,470)	1.20 \pm 0.43 (0.62–1.98)	1.73 \pm 0.60 (1.13–2.95)	275 \pm 67 (191–400)
Intermediate moan (n=34)	Sebastian	270 \pm 103 (122–592)	457 \pm 89 (328–750)	744 \pm 247 (469–1,163)	1,917 \pm 1,054 (984–4,875)	4,890 \pm 567 (3,350–5,796)	0.82 \pm 0.27 (0.31–1.59)	1.21 \pm 0.41 (0.49–2.14)	308 \pm 36 (219–381)
Brief moan (n=26)	Sebastian	312 \pm 106 (41–456)	447 \pm 88 (258–563)	773 \pm 463 (258–2498)	2,205 \pm 1,020 (904–4,828)	4,490 \pm 927 (2,031–5,903)	0.41 \pm 0.14 (0.13–0.64)	0.59 \pm 0.18 (0.20–0.91)	296 \pm 40 (199–373)
Croak (n=171)	Pearl	320 \pm 426 (0–2377)	1,157 \pm 679 (234–2,531)	1,982 \pm 911 (234–5,484)	4,204 \pm 1,739 (1,031–10,547)	6,718 \pm 2,570 (3,337–12,441)	0.10 \pm 0.07 (0.02–0.54)	0.17 \pm 0.08 (0.07–0.69)	–

used as predictors and sound categories as the response. RF models were used due to their high prediction accuracy and non-parametric inferential properties (Breiman 2001; Hastie et al. 2009). The predictive performance of RF model is not influenced by the amount of multi-collinearity among variables largely because in RF not all variables are considered simultaneously when building trees, but only some of randomly selected variables are considered (Hastie et al. 2009; James et al. 2013). Hence, there is no need to remove collinear variables for the RF model predictive performance. However, when exploring the relative importance of variables on explaining a dependent variable one might get the wrong impression of important variables, if strongly correlated variables are retained as they will “compete with each other in explaining the dependent variable” (Lin 2020) and impact RF model’s ability to accurately identify strong predictors (Gregorutti et al. 2017). Thus, it was important for our study to deal with multi-collinearity to produce accurate indices of variable importance.

Prior to fitting RF models, we tested for multi-collinearity between our predictor variables (minimum (0% and 5%), peak and maximum (95% and 100%) frequencies, 90% and 100% duration and PRR) using generalised variance inflation factor (GVIF; Fox and Monette 1992). The highest GVIF was 61 when all variables were considered, indicating strong multi-collinearity between predictor variables. The GVIF decreased to 2.68 when 0% minimum frequency, 100% maximum frequency, 100% duration and peak frequency were used as predictors, which indicated no multi-collinearity, therefore these variables were used in the RF models.

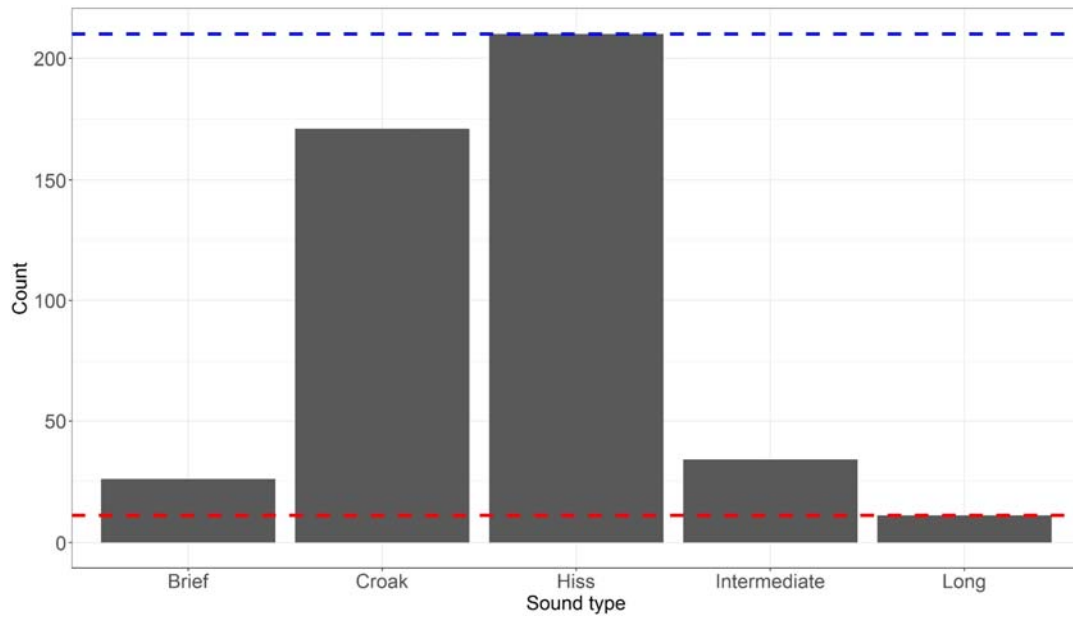


Figure 2. Count (sample sizes) of each sound type from the original (unbalanced) data (bar plots). Horizontal blue dashed line represents sample size of ADASYN, SMOTE and upsampling sample balancing methods, whereas red dashed line represents sample size downsampling sample balancing method. Long represent long moan calls, intermediate represents intermediate moan calls and brief represents brief moan calls.

Due to noticeable difference in sample sizes of sound types (Figure 2), we assessed the influence of class imbalance on the overall and class specific accuracy. This was done by using four methods of addressing class imbalance [Synthetic Minority Over-sampling TEchnique (SMOTE; Chawla et al. 2002), ADAptive SYNthetic (ADASYN; He et al. 2008), downsampling and upsampling (Nallamuthu 2020)] as shown in Figure 2. All balancing methods passed the correlation threshold of 0.8 except for downsampling (Appendix C: Figure C1), thus downsampling was excluded from classifying sound types and estimating variable importance. Tuning of RF model parameters was performed based on 70% of the original data as a training set, and the balance was used for testing. After tuning, RF model performance scores were determined using multi-class accuracy metric (Chaudhary et al. 2016). Mean decrease in accuracy was used to determine which of the predictor variables (sound characteristics)

best described the sound classification in the RF models. Mean decrease in accuracy articulates how much accuracy the RF model losses by excluding each variable. The more the accuracy lost, the more important the variable is for the successful classification.

Detection and characteristics of hisses under different behavioural contexts - Ragnar

As the most commonly detected sound type, the detection and characteristics of hisses were analysed in further detail and confirmed through observations of behavioural contexts. Detected sounds from Ragnar were classified into five contextual sessions: no session, pre-feed, pool feed, post-feed, and transportation preparation (Appendix D: Table D1). For all five sessions, the 100% duration of hisses was measured to evaluate if this changes with associated potential arousal state: high arousal contexts (pre-feed, pool feed, and transportation preparation) or low arousal contexts (no session and post-feed). Production rates (hisses per minute) were calculated for each recording session by dividing the number of hisses within each recording session by recording durations in minutes. Differences between sessions for both hiss duration and production rate were tested with multiple pairwise t-test comparisons (with Bonferroni adjustment as a multiple testing correction) using the 'rstatix' package (Kassambara 2021) in R.

Diel patterns in hiss production - Pearl

Diel patterns in hiss production rates (calculated as above) were assessed for Pearl where the length of continuous recording sessions were 24 hours or more (Table 2). Since time of day is a circular variable, hiss rates of Pearl were smoothed through penalized cyclic cubic regression splines (Wood, 2017) of generalized additive models (Guisan et al. 2002) to establish diel pattern of hissing. Citizen scientists observed the

seal for over 109 hours to estimate diel pattern of occurrence of activities: active (moving around, swimming, feeding, rolling) or resting (sleeping, not moving around or briefly awake). A detailed description of the citizen scientists' observations is provided in Appendix E. Times of daylight, twilight (dawn and dusk) and night-time were downloaded from <https://www.timeanddate.com/sun/south-africa/port-elizabeth> to indicate daylight regime (Appendix E) of diel activities and hiss production patterns of Pearl.

Behavioural context, individual differences, and conspecific interaction

Smartphone video (Video A1) data were collected by an observer positioned in front view of Sebastian and Ragnar within 5 m from the seals. Ragnar was kept and recorded in Durban before transfer to Gqeberha to be with Sebastian for one day before their simultaneous release into the wild, so an opportunity to document conspecific interaction (Tables 1 and 2). Durations of these behavioural context observations are equivalent to recording durations in Table 2. These data were used to observe the behavioural context of call production and generate hypotheses about call function. Individual differences in sound occurrence and usage as observed in real time and through video analysis, and were described qualitatively and quantitatively to estimate mean sound production rate for Sebastian alone and with a conspecific.

Results

Overall, there were 136 hours of acoustic recordings (Table 2). More recording effort was available for Pearl (130.43 hrs) compared to Ragnar (2.45 hrs) and Sebastian (1.07 hrs) or both Ragnar and Sebastian in the same pen (2.64 hrs). Underwater sound recording was limited to Ragnar; however, no underwater sounds were detected from the 1.28 hour acoustic recordings.

Repertoire and classification of in-air sounds

A total of five sound types (brief, intermediate and long moan calls, croaks, and hisses) were identified, with the hiss sound being the most frequently detected (Figure 1, Table 3). To avoid confusion with the nomenclature of the already described underwater crabeater seal calls (i.e., the short moan call, Shabangu and Charif, 2021), we use the term “brief” to describe the aerial (or in-air) moan call with the shortest duration (Table 3, Appendix A: Table A1). Hisses were detected from all seals, Sebastian and Pearl produced moan calls, and croaks were only produced by Pearl. *Ad hoc* comparison showed that the 90% and 100% duration of hisses recorded from Ragnar and Pearl were significantly longer than those of Sebastian (Welch t-test: $P < 0.05$), whereas moan calls of Sebastian and Pearl were spectrally comparable. Balanced RF models performed very well at classifying all sound types with 80-100% agreement between the true measurement (Table 3) and RF model prediction, and there was little to no confusion with other sound types (Figure 3(a–c)). However, a misclassification error rate up to 80% was found in RF model with unbalanced sample sizes (Figure 3(d)). Global RF models with different sample balancing methods indicated that the 100% duration was the most important variable for classifying brief, intermediate and long moan calls, and croaks, as well as overall sound classification (Figure 4). The 0% minimum frequency, 100% maximum frequency and peak frequency were moderately important characteristics for classifying brief, intermediate and long moan calls, and croaks (Figure 4). For hisses, the 100% maximum frequency was the most important predictor (Figure 4) as hisses extended up to 47 kHz whereas all other sound types were constricted to <13 kHz.

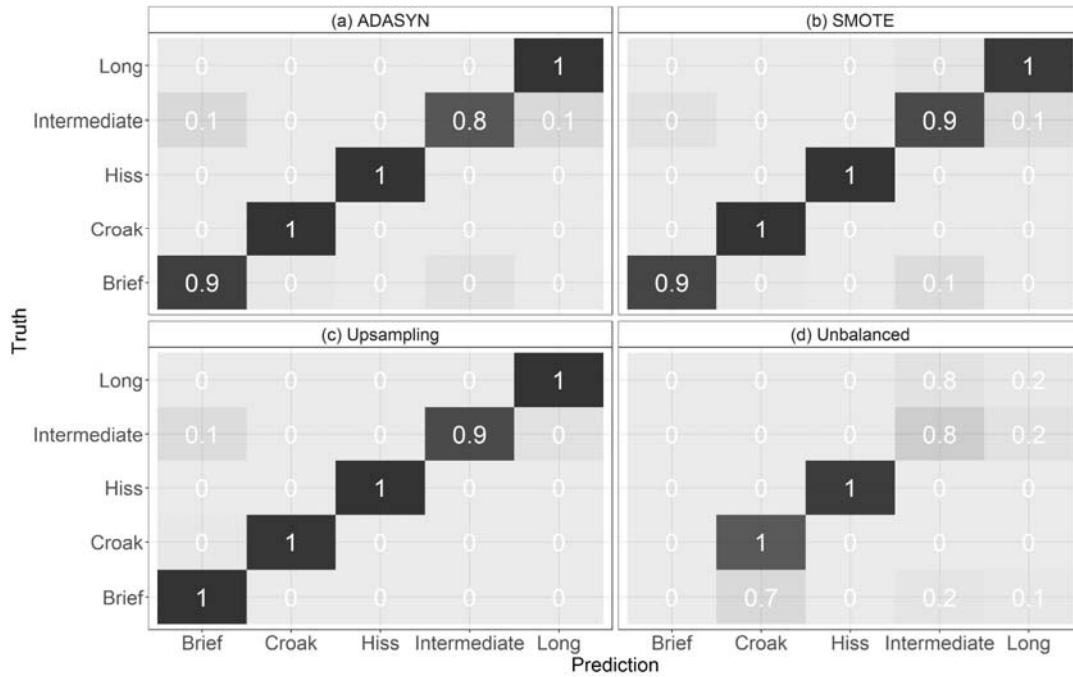


Figure 3. Confusion matrices of sound classification according to prediction versus measured (truth) characteristics of all juvenile crabeater seal sound types based on (a) ADASYN, (b) SMOTE, (c) upsampling and (d) unbalanced methods. Long represents long moan calls, intermediate represents intermediate moan calls and brief represents brief moan calls.

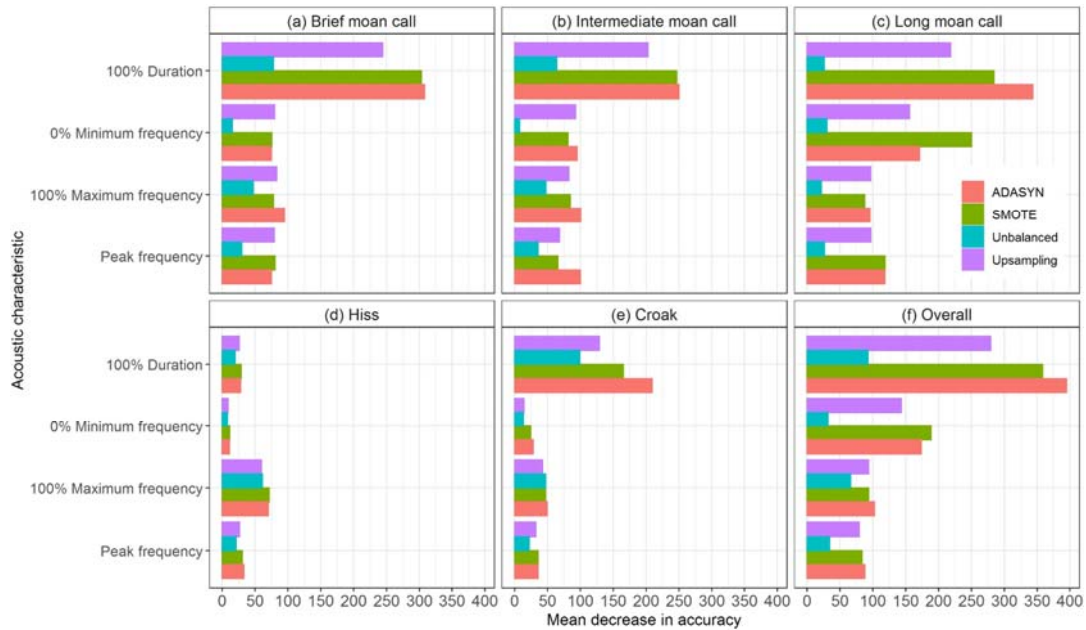


Figure 4. Mean decrease in accuracy of acoustic characteristics at classifying sound types of juvenile crabeater seals according to different sample size balancing methods.

The pulses of few in-air moan calls produced by these juvenile crabeater seals had generally similar waveform characteristics to those of the underwater short moan calls produced by seal of unknown age presented in Shabangu and Charif (2021). The 90% duration of all in-air moan calls were significantly shorter than their underwater counterparts (Welch t-test: $P < 0.05$), while the PRR of in-air moan calls were significantly slower than those of underwater types (Welch t-test: $P < 0.05$). The 5% minimum frequency of all in-air moan calls were significantly lower and higher than underwater high and low moan calls respectively (Welch t-test: $P < 0.05$). The 95% maximum frequency of all in-air moan calls was significantly lower than high moan calls (Welch t-test: $P < 0.05$) but comparable to those of low and short moan calls (Welch t-test: $P > 0.05$). The peak frequency of in-air brief and intermediate moan calls was significantly different from all three types of underwater moan calls (Welch t-test: $P < 0.05$), whereas long moan call peak frequency was not significantly different to underwater low and short moan calls (Welch t-test: $P > 0.05$).

Detection and characteristics of hisses under different behavioural contexts- Ragnar

In total, 298 hisses were recorded from Ragnar during his overall stay in the Durban rehabilitation centre. Hiss production rates were not significantly different between sessions of interacting with animal care staff, although the pre-feed session had the highest median sound rate, and the no session period had the lowest median sound rate (Appendix F: Figure F1). Hisses with significantly longer duration were detected during pre-feed and transport preparation, hisses detected during the no session and post-feed period had comparable durations, and hisses detected while feeding had the shortest duration (Figure 5).

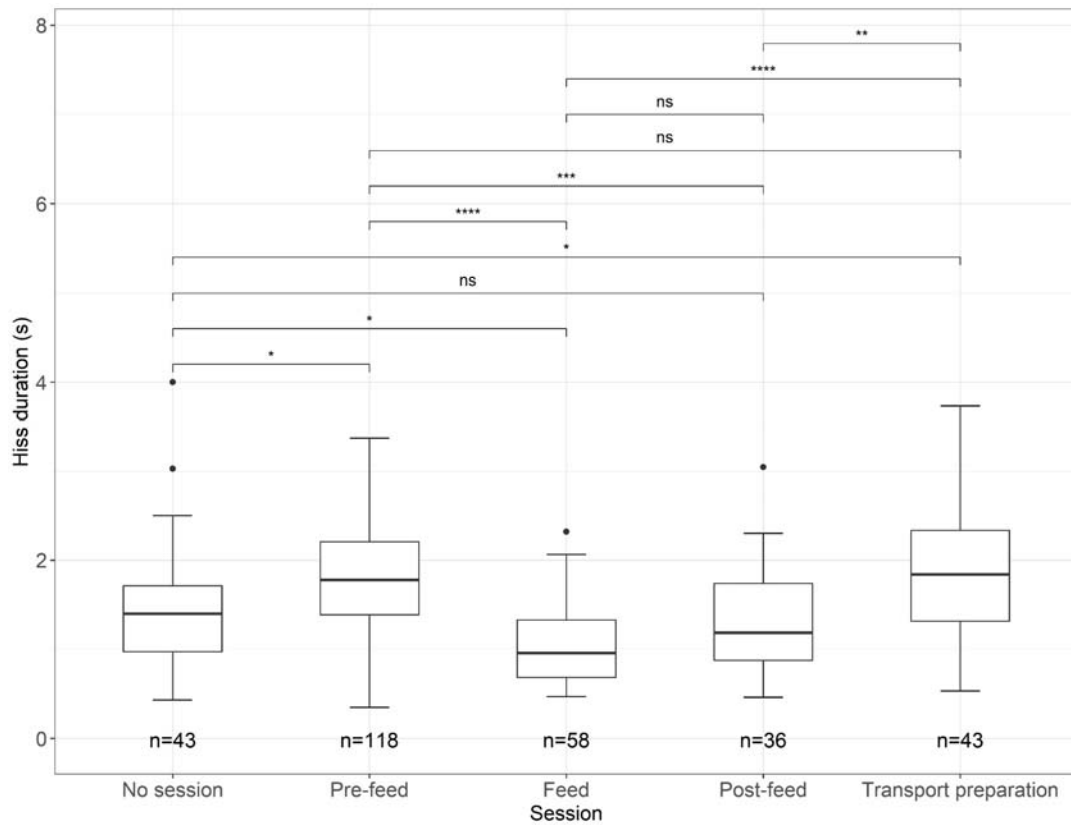


Figure 5. Box and whisker plot of hiss sound 100% duration produced from different recording sessions in Durban. Significance levels: ns represents not significant ($P > 0.05$); * for $P < 0.05$; ** for $P < 0.01$; *** for $P < 0.001$. Boxes signify the interquartile range (i.e., the first to the third quartile), black horizontal line inside boxes specify medians, and closed circles are hiss rates that are outside the range covered by whiskers. Whiskers indicate 1.50 times the interquartile width. n is the sample size of hisses measured.

Diel patterns in hiss production - Pearl

Overall, 24,324 hisses were recorded from Pearl over 12 different recording sessions.

Hisses were produced throughout the day with lower production rates during the daylight hours (mean rate of 2.46 hisses per min; maximum rate of 15 hisses per minute) when the seal was more active as observed by citizen scientists, and greater production rates at night (mean rate of 3.65 hisses per min; maximum rate of 16 hisses per minute) when the seal was at rest (Figure 6). There was no difference in the duration of hisses produced by Pearl in the presence or absence of human observers

(Welch t-test: $P > 0.05$). However, in the absence of human observers, hisses during the day were longer than at night (Welch t-test: $P < 0.05$). The ISI of hisses during daytime (109.11 ± 59.27 s; range: 23.46 s–5.36 minutes; $n = 111$) was on average longer than those measured at night-time (75.08 ± 38.51 s; range: 25.09 s–3.46 minutes; $n = 104$) but IHI were shorter during the day (4.05 ± 1.37 s; range: 1.51–9.76 s; $n = 101$) compared to at night (5.64 ± 2.42 s; range: 1.91–11.45 s; $n = 153$).

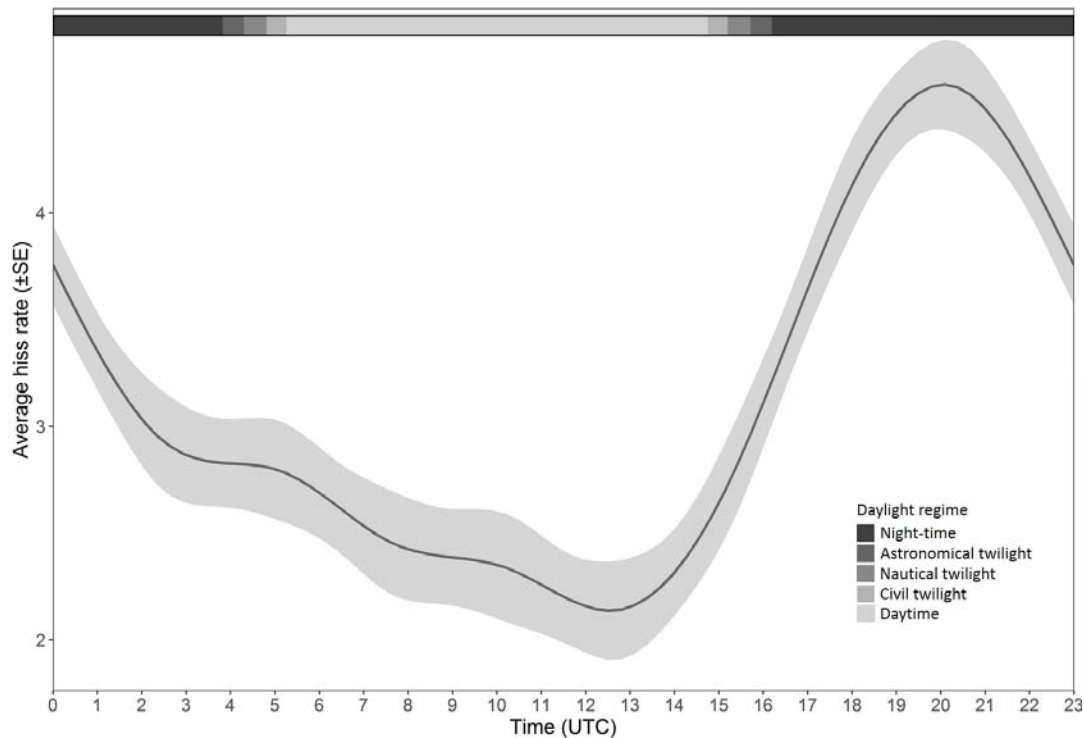


Figure 6. Circular smoothed diel pattern of hiss rates (sounds per minute) for each hour from all recording sessions of Pearl in Gqeberha. Horizontal bar shading indicates daylight regime as defined in the key. Line plots represent average hiss rates, and grey shaded regions around line plots represent the standard error (SE) of those averages. UTC is Coordinated Universal Time.

Behavioural context, individual differences, and conspecific interactions

From *ad hoc* recordings, 72 sounds were opportunistically detected from Sebastian with human presence. Those sounds consisted of 23 brief moan calls (representing 34% sound use), 17 intermediate moan calls (25% sound use), one long moan call (2% sound

use), and 26 hisses (39% sound use). A total of 656 sounds were recorded when Sebastian and Ragnar were in the same pen, which consisted of 49 brief moan calls (7% sound use), 93 intermediate moan calls (14% sound use), 57 long moan calls (9% sound use) and 457 hisses (70% sound use). Sebastian produced moan calls (all three variations) and hisses while Ragnar only produced hisses (Video A1). Hiss rate was higher (average of 6.8 hisses per minute) for the first 15 minutes when Ragnar was introduced into the pen, and then decreased to an average of 2.5 hisses per minute for the remaining 2.39 hours of recording.

Pearl started producing sporadic series of croak calls concurrently with an open mouth display at dawn before feeding sessions, and the production of croaks was only documented towards the end of the recording period (18 June onwards– Table 2). Average ICI was 0.08 ± 0.06 s (n= 128) and ranged from 0.01 to 0.33 s. Average number of croak pulses per series was 7.13 ± 3.52 (n= 24) with a range of 3 to 17 (e.g., Figure 1(c)).

Discussion

Our study provides novel information on the acoustic repertoire of a fourth Antarctic phocid seal (in addition to leopard *Hydrurga leptonyx*, Ross and Weddell seals) to produce in-air and underwater sounds. This study contributes towards the understanding of how juvenile crabeater seals acoustically interact with conspecifics and of general sound use in-air, which is important for the in-air acoustic ecology of the species. We provide the first evidence of in-air moan calls and croaks of crabeater seals, as well as characteristics of hisses, with evidence that these sounds are dynamic, and may vary inter-individually and across contexts.

Comparable characteristics of sounds collected using opportunistic recorders (smartphones) and those collected using a dedicated acoustic recorder (handheld microphone), indicate that opportunistic recorders such as smartphones can be successfully used to study the acoustic repertoire of the species in absence of dedicated recorders although some limitations/hurdles such as low sampling rates still need to be overcome (e.g., Faber 2017; Brambilla and Pedrielli 2020). On the other hand, RF models validated that in-air sounds of crabeater seals can be correctly classified mainly using the sound duration whereas other acoustic characteristics such as minimum, maximum, and peak frequencies can be added to slightly improve the overall classification accuracy. Moreover, RF model classification quantitatively supported our visual classification of sounds into types.

Ragnar did not produce moan calls when held at either of the locations, which conforms to previously observed non-vocalizing behaviour of this species in-air (Nel 1966; Cline et al. 1969). On the other hand, in-air vocalizations produced by Sebastian and Pearl differed from previously documented and expected acoustic behaviour for this species, reflecting that the acoustic behaviour of crabeater seals remains mostly unknown. For example, the detection of croaks from Pearl further indicates our incomplete knowledge of this species' acoustic repertoire and communication system that is dynamic and more complex than previously thought. It is intriguing that Pearl produced croaks only at dawn and in the early morning but not at any other time of the day as she did with hisses. This behaviour, as observed by citizen scientists, seemed to be indicative of arousal before the first feed of the day. Call properties of croaks are different to those of moan calls and hisses, suggesting that this call type might be produced for a specific purpose.

The 90% duration, 5% minimum frequency and 95% maximum frequency of all three in-air moan call types produced by juveniles were significantly different from their underwater counterparts (Klinck et al. 2010; Shabangu and Charif 2021), suggesting that these may be specifically produced for in-air communication. Contrary to underwater moan calls, in-air moan calls detected in our study did not contain sidebands below and above the carrier frequency at the beginning of the call (Figure 1(b)), which might be another adaptation for vocalizing in-air. Peak frequencies of long moan calls detected in this study are analogous to those determined for underwater low moan call (Klinck et al. 2010) and short moan call (Shabangu and Charif 2021), reflecting that the energy of most of these calls is located at similar frequency band. Significant difference between peak frequencies of in-air brief and intermediate moan calls and underwater low, high, and short moan calls suggests that energy of these calls is positioned in different frequency bands.

The influence of age may impact direct comparison of in-air (juveniles in rehabilitation) and underwater (wild individuals of unknown age) sounds. However, the peak frequency of calls of other pinnipeds such as southern elephant seals *Mirounga leonina* (Sanvito et al. 2007) and harbor seal *Phoca vitulina* pups (Ravignani et al. 2017) is negatively correlated to body size. This suggests that our studied seals may be of similar sizes to some of those detected off the Ekström Ice Shelf (Klinck et al. 2010) and Maud Rise (Shabangu and Charif 2021) in Antarctica.

Ragnar's hiss production rates suggest that he might have been initially highly aroused when animal care staff first appeared for feeding, possibly in anticipation of food, but became calmer towards the end of feeding. Similar arousal behaviour was observed from Pearl whereby she produced a series of croak calls before feeding towards the end of the study period. Bottlenose dolphins (*Tursiops* spp.) in human care

were also observed to be aroused acoustically before feeding (Probert et al. 2021). The duration of hisses significantly increased when seals appeared to be more aroused. For example, significantly longer duration hisses with lower minimum frequencies were detected from Ragnar when he was interacting with animal care staff during different sessions in Durban, than when interacting with Sebastian in Gqeberha. Both moan calls and hisses produced by Sebastian were used in an antagonistic manner (open-mouth and teeth bared displays) towards Ragnar. Percentage use of hisses from Sebastian in human presence was lower compared to hiss production when sharing a pen with Ragnar, suggesting an increased arousal state in the company of a conspecific. These seals were occasionally observed to hiss with an open-mouth display in the presence of both humans and conspecific during rehabilitation, which has been previously observed in the wild and defined as an antagonistic display for this species (Nel 1966; Cline et al. 1969). In the wild, males courting females with pups have been observed to aggressively drive away other males who approached these groups in ice floes using hisses, whereas females with pups used hisses to drive away males trying to separate them from their pups (2021 email conversation from T Rogers to FWS; unreferenced). Another purpose of the hisses may be to clear away mucus in the nasal passages (Hofman 1975), as both Pearl and Sebastian were observed to produce copious amounts of nasal discharge, possibly due to mites, as found in the nasal passages of many species of pinnipeds (e.g., Dailey 2001).

Hisses were produced by Pearl in two contexts: at night in the absence of humans when she was likely sleeping, and during the day in the presence of humans while awake or asleep. This indicates that sounds with the same acoustic properties may be used as an acoustic response to a particular situation and may be a by-product of exhalation. The difference in durations ISI and IHI between day and night might reflect

different motivations to hiss between these contexts. The average IHI suggests that juvenile seals could experience apnea when active for an average of 1.82 minutes to a maximum of 5.36 minutes on land during the day, and an average of 1.3 minutes to a maximum of 3.47 minutes while sleeping at night. These average apnea periods on land are significantly shorter compared to the average underwater apnea duration of 4.6 minutes (range: 0.2–23.6 minutes) for crabeater seals during dives in the wild (Burns et al. 2004). These differences could be age related, as adult animals were the subjects of Burns et al. (2004) and due to faint hisses being undetected by the recorder. The period of apnea is expected to be longer when pinnipeds are sleeping than when they are awake in the wild (Wartzok 2009); however, Pearl's results show a different apnea pattern likely because she was not always producing hisses during each breathe. She was mostly awake during the day, whereas she would mostly be asleep at this time in the wild (e.g., Burns et al. 2004). These differences are likely due to the seal's adaptation to rehabilitation environment where night-time foraging was not necessary, but food was provided on schedule during the day and therefore expected during this time. In addition, there was far greater activity and therefore possible stimulation in the rehabilitation environment during the day. The switch to greater activity during the day was indicated by the observation that all of the seals were initially uninterested in food provided during the day, only eating in the evening.

Assuming that hisses are produced at every exhalation, estimation of breathing pattern of these seals through these multi-purpose hisses, suggests that the health and welfare of these animals can be studied through passive acoustic monitoring if they are close enough and the average breathing rhythm of an age group is known. Frequency of breathing is used for monitoring health condition in other species of mammals (Brown-Brandl et al. 1998; Gaughan et al. 2000; Srikandarkumar and Johnson 2004), including

marine mammals (St Aubin and Dierauf 2001; Jensen et al. 2013). Hofman (1975) observed a breathing rate of 8–11 breaths per minute for tranquilized adult crabeater seals when resting, which is lower than maximum breathing rate estimated from Pearl while resting/sleeping at night by this study (16 hisses per minute).

Sebastian and Pearl were observed to always produce moan calls with mouth open, which suggests that these seals might produce these calls in a similar way underwater as observed for vocalizations of leopard seals produced in-air and underwater (Rogers et al. 1995). Vocalizing with the mouth open likely doubles the diameter of the vocal tract and increases the frequency of the call, making those calls louder, as detected for southern elephant seals (Sanvito et al. 2007). Similarly, Pearl was observed to produce croaks with mouth open, likely to make calls louder. Our observation of Sebastian using moan calls when sharing a pen with Ragnar, suggests that moan calls may be used for territorial defence, as Sebastian produced moans with concurrent observed antagonistic behaviour when Ragnar was introduced into his pen'. Both Sebastian and Pearl were heard producing many moan calls when they first arrived in Gqeberha but decreased their call rates over time during their rehabilitation, perhaps because of the absence of conspecifics or they may have become more habituated to the rehabilitation facility and did not perceive the animal care staff as a threat anymore. This decrease in call rate implies that this sound type might also be used for cohesion with conspecifics or used during stressful events such as going into a new environment. The observation of both male (Sebastian) and female (Pearl) seals producing in-air moan calls in rehabilitation challenges the assumption that underwater moan calls are produced by males only (van Opzeeland et al. 2010).

Average characteristics of hisses recorded from Ragnar and Pearl were different from those of Sebastian, indicating inter-individual variability. Differences in acoustic

behaviour and acoustic repertoire between the Ragnar, Pearl, and Sebastian are likely due to inter-individual variability where Ragnar did not produce moan calls compared to the other two seals. Inter-individual variability has also been observed in Weddell seals (Terhune et al. 1994). Croaks were only detected from Pearl, another indication of inter-individual differences in vocalizing behaviour. The variation in ICI and number of pulses within croaks might be related to behavioural context, in this case, arousal before feeding. Our study shows that the acoustic repertoire of these seals is not monotonous but is diverse, dynamic, and varies among individuals.

Conclusions

We provide the first description and characteristics of in-air moan calls, croaks, and hisses of juvenile crabeater seals, which updates the current knowledge of the acoustic repertoire and acoustic behaviour of this species. This study improves our knowledge of the acoustic communication of crabeater seals when interacting with conspecific and humans and when alone. Following the acoustic responses of these seals to human presence observed in this study, human presence and interactions should be reduced as much as possible around important habitats of these seals by developing minimum distance guidelines to approach them. The rare occurrence of these three juvenile crabeater seals afforded us an opportunity to describe some aspects of the in-air acoustic repertoire and acoustic behaviour of this relatively poorly known Antarctic species. Results of this study may be applicable beyond the rehabilitation environment into the natural habitats of these seals given that animals studied here spent a short time in rehabilitation and most likely exhibited aspects of their natural or wild behaviours.

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Ethical statement

Ragnar was captured and rehabilitated under Permit No. S03156 issued to the South African Association for Marine Biological Research by the Department of Forestry, Fisheries and the Environment (DFFE) in terms of the National Environmental Management Biodiversity Act 2004 (Act 10 of 2004). Sebastian and Pearl were captured and housed under Permit No. S03169 in terms of the National Environmental Management Biodiversity Act 2004 (Act 10 of 2004) and Permit No. RES2021-29 issued to the Port Elizabeth Museum at Bayworld by the DFFE in terms of the Marine Living Resources Act 1998 (Act 18 of 1998). Both facilities are accredited members of Pan African Association of Zoos and Aquaria. All individuals observed in this study were captured, transported to the rehabilitation facilities, rehabilitated, and later released alive at sea, with due regard to animal welfare by experienced staff.

Data availability

Most data are available in the main text, and provision of raw data will be considered on a reasonable request.

Declaration of interest

The authors declare no competing interests.

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Appendix

Appendix material of this paper can be found online at (to be provided at a later stage).

Link to video: <https://drive.google.com/file/d/1z1f7Z2n9iN7czKiUY5p493hQpW-kpXCX/view?usp=sharing> and can be downloaded:

<https://doi.org/10.5281/zenodo.4743566>

Video A1. Interaction between Sebastian (left) and Ragnar (right) in the same pen at Bayworld Oceanarium, Gqeberha. Video taken by Maëlle Connan.