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Leopard seal song patterns have similar predictability to nursery rhymes

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During their breeding season, male leopard seals (*Hydrurga leptonyx*) spend hours perfecting their solo performance: singing unique sequences of stereotyped calls underwater to create their 'song'. These song bouts are made up of discrete call types common across leopard seals within a region, which begs the question – what determines the individually unique patterns of these calls? Information entropy quantifies the amount of randomness in a sequence, providing insight into the statistical patterns governing a sequence. The songs produced by 26 different Eastern Antarctic leopard seals have less predictable temporal structure than humpback whale songs and dolphin whistle sequences. The estimated information entropy of the leopard seal songs is comparable to nursery rhymes but unsurprisingly, lower than contemporary, classical and baroque music. The greater structure of the leopard seal's song improves the ability of distant listeners to accurately receive signals and identify singers, which is essential for this widely dispersed species. Future studies examining animal mating song would benefit from incorporating entropy analysis to question if information is conveyed through temporal structure alongside other acoustic variables.

Keywords Signal propagation, Animal communication, Marine mammals, Territorial signalling, Mating calls, Sexual signalling

Humans are far from the only animals to employ singing as a method of communication - animals sing for several purposes including territorial signalling, mate attraction or warning of predators¹. While many bird species are known to produce complex and elaborate vocalisation bouts (hierarchically constructed of various 'notes', 'elements', 'syllables', 'phrases' and 'motifs')² comparatively few mammals have been observed to assemble various vocal units or discrete sounds into more complex sequences. Examples of those that do include the 'songs' of rock hyraxes (*Procavia capensis*)³, free-tailed bats (*Tadarida brasiliensis*)⁴, gibbons (*Hylobates*)^{5,6}, mice (*Mus musculus*)⁷ and humpback whales (*Megaptera novaeangliae*)^{8,9}, the alarm calls of orangutans (*Pongo pygmaeus*)¹⁰, the 'chuck' calls of squirrel monkeys (*Saimiri sciureus*)¹¹, the 'codas' of sperm whales (*Physeter macrocephalus*)^{12,13}, the whistle sequences of killer whales (*Orcinus orca*)^{14,15} and short-finned pilot whales (*Globicephala macrorhynchus*)¹⁶, and 'bray' sequences of bottlenose dolphins (*Tursiops truncatus*)^{17,18}. We theorise that highly vocal pinnipeds (seals and sea lions) who produce sequential vocalisations may also be ideal candidates for information theory analysis, specifically the vociferous leopard seal.

Leopard seals are vocal during the mating season, with male leopard seals making sequences of loud stereotyped sounds underwater for the purposes of mate attraction and territorial signalling^{19–22}. Vocal displays have been observed in phocid species when the oestrus females are inaccessible to males, and in the case of leopard seals this is due to the females remaining hauled out with their pups until weaning²³. Leopard seal calling behaviour is common during December and January, which coincides with their breeding season²⁴. Both male and female leopard seals in captivity have been shown to cease their calling behaviour with the drop in their reproductive hormones¹⁹ suggesting that the calling behaviour is an important component of mating behaviour in the leopard seal¹⁹.

Male leopard seals are solitary during spring/summer^{25–27}. It is theorised that for male leopard seals, their sparse distribution amongst the pack ice and the shortness of their breeding season increases this calling behaviour, as they call for many hours each day throughout the breeding season to increase their chances of their calls being received²⁸. Additionally, the use of vocal displays to advertise to potential mates or to communicate information about individual identity is much more energetically efficient than travelling wide distances for species with wide dispersal. As leopard seals are often widely and unpredictably dispersed²⁹ long range acoustic

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displays are necessary. As such, the leopard seals' communicative ability benefits from the use of a small repertoire of stereotyped sounds which are easily recognisable despite degradation or propagation effects^{23,28}. This consistency of calling behaviour and stereotypy of sound types within a population makes leopard seals an ideal candidate for information theory analysis to examine their song structure.

The male leopard seals will vocalise underwater, producing a sequence of sounds in a distinct pattern before returning to the surface to breathe, creating breaks of silence in their singing cycle¹⁹. While there is geographic variation in acoustic behaviour between populations of leopard seals^{20,30} the alphabet of sounds within a population remains consistent³⁰. In the coastal region of the Davis Sea, Eastern Antarctica, leopard seals produce sequences of sounds, or 'calling bouts', made up of an alphabet of 5 distinct stereotyped calls (Fig. 1) which range in frequency from 50 Hz to 6 kHz, and between 0.5 and 8.1 s in duration^{19,20}. The 5 call types are classified as high double trills (H), medium single trills (M), low descending trills (D), low double trills (L) and a hoot with a low single trill (O)^{20,31}.

While the acoustic characteristics of the sounds themselves show very little variation between individuals, the order individual seals produce sounds within a sequence varies³¹. The lack of stereotypy in sequencing between individual leopard seals motivates the need for probabilistic techniques to understand this variation. To analyse the leopard seal vocalisations, we have recorded sequences produced by individual seals and converted them to a symbolic code (Fig. 2).

Many studies have made comparisons between marine mammal communication and human language structures, suggesting that marine mammal communication can have 'language-like' properties^{32,33}. Borrowing concepts from human music theory can also prove to be a useful comparison to marine mammal communication^{9,12,34,35} as it does not assume any semantic meaning is contained within each individual sound. While a number of musical characteristics such as chord progressions, note duration or rhythmic elements could be compared to leopard seal songs (and analysed with information theory techniques)³⁶ melodic contour (or the sequence of 12 notes that make up the melodic scale in Western music) is the most analogous to the symbolic code representing leopard seal vocal sequences.

Shannon's 'information entropy' measures the uncertainty of a random variable³⁷. In the context of communication, entropy is an upper bound on the amount of information contained within a sequence³⁸ (however entropy is not necessarily a measure of complexity of the sequence or source³⁹). Information theory³⁷ provides insight into the structure of an information source (often referred to as 'syntax' or 'grammar' in communication) without assuming any knowledge of the meaning (or 'semantics') of the source output. A sequence with higher entropy is more random, or less predictable, than a sequence with lower entropy. If the true probability distribution of a vocalizing animal were known, the entropy could be computed directly. However, since these true distributions are not known, both parametric and nonparametric methods can estimate entropy. When comparing two entropy estimators for a source, the estimator whose model would better predict data from that source will result in the lower entropy estimate. Thus, the estimator with the lower entropy estimate is a better match for the structure of the source.

Our first parametric entropy estimator assumes that all calls in the sequence are independent and identically distributed (i.i.d.). This model is equivalent to flipping a weighted coin a certain number of times in a row – not all outcomes are equally likely, but each new flip is completely random. Knowing the previous symbol does not improve our ability to predict the next symbol.

The second parametric model is the first-order Markov model, which assumes that the choice of each sound depends only on the sound which comes directly before it. In the field of music, Markov chains have been investigated for their potential for generating compositions, evaluation of musical complexity and composer/period identification^{40–46}. Although he was far from the first, Wolfgang Amadeus Mozart was rumoured to have invented a game in which a pair of dice are used to select segments of pre-composed waltz-like music to create a new piece which sounded, to an untrained ear, like a waltz written by Mozart himself^{47,48}. As a 1st order Markov model output assumes dependence on only the single preceding symbol, an n th order Markov model assumes that the output is dependent on the previous n symbols.

i.i.d. and Markov chain models are limited by underlying assumptions and cannot accurately capture the longer term dependencies in hierarchically structured sequences⁴⁹. Many animal sequences are better represented by other non-Markovian processes⁴⁹. Hence, we also applied the nonparametric sliding window match length (SWML) entropy estimator^{50–52}. The SWML entropy estimator relates the entropy of a given output sequence to the average length of a matching string of units within a window of fixed size. The SWML estimator can highlight the presence of longer patterns in the sequence, i.e. structure that is more complex than relating one unit to its preceding unit.

If the temporal structure of the leopard seal calling bouts could be explained by an i.i.d., then we would expect the 1st order Markov entropy estimates not to be significantly lower than the i.i.d. estimates. Similarly, if the structure of the calling bouts could be explained by a 1st order Markov model, we would expect the SWML estimates not to be significantly lower than the Markov model estimates.

Do the songs of leopard seals have predictable sequence structure? And if so, how does this structure compare with that of other mammals? Here we examine the vocal sequences of 26 leopard seals and compare entropy estimates with those of other mammals including humpback whales, bottlenose dolphins and squirrel monkeys, and with simplistic representations of human music, to understand the similarities between vocal communication structure across taxa.

Results/Discussion

For all leopard seal calls analysed, the entropy estimates were lower than the theoretical maximum entropy for the size of the source alphabet, from which it can be inferred that the choice of sounds in the sequence is not

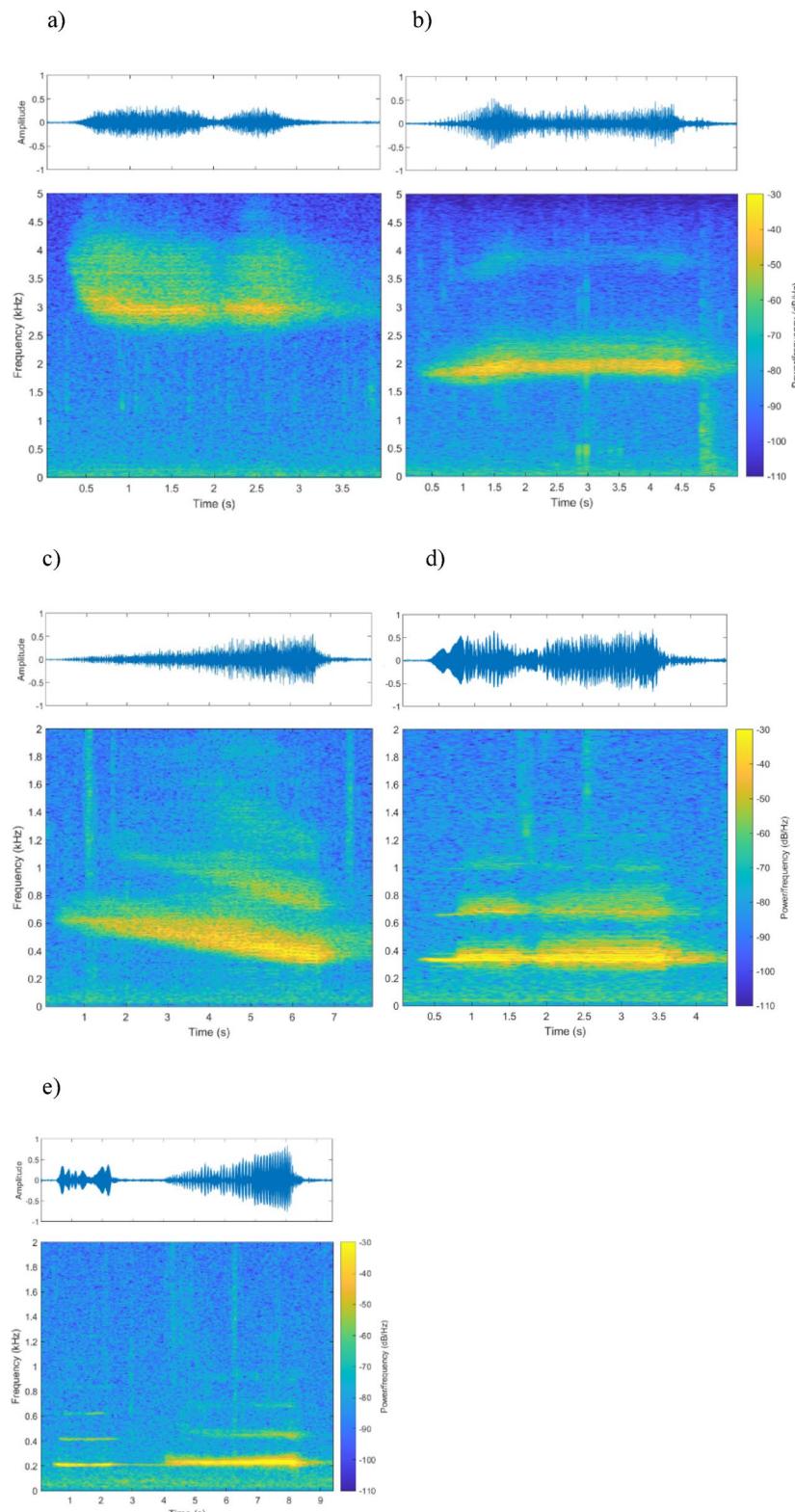


Fig. 1. Waveforms and spectrograms of leopard seal underwater call types (2048 ppt, 90% overlap, Hanning window): **(a)** high double trills (H), **(b)** medium single trills (M), **(c)** low descending trills (D), **(d)** low double trills (L) and **(e)** a hoot with a low single trill (O).

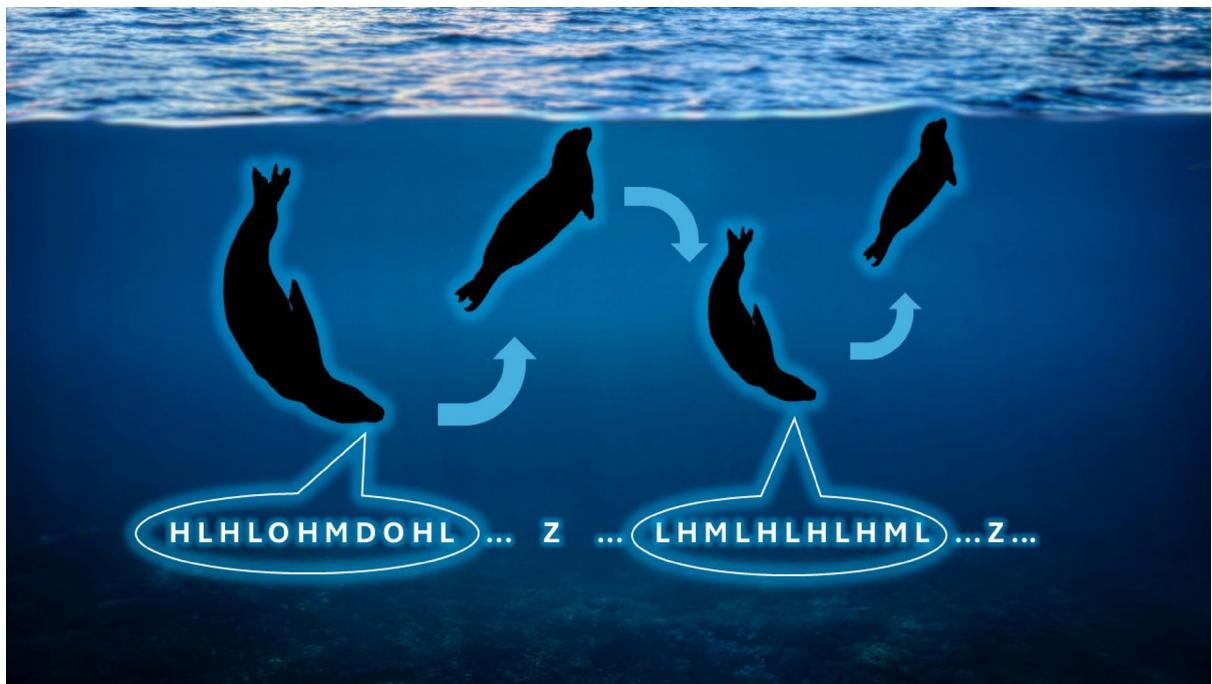


Fig. 2. Typical behaviour of leopard seal vocalisations - the male will sing a sequence of sounds underwater before returning to the surface to breathe (represented by a 'Z') and repeats this cycle for hours at a time. The sequence of sounds is then converted to a symbolic code (Microsoft PowerPoint Version 2505).

entirely random. For the 26 leopard seals analysed, the i.i.d., 1st order Markov and SWML entropy estimates ranged from 1.59 to 2.38, 0.72–1.43 and 0.63–1.38 bits respectively (Table 1; Fig. 3).

For all leopard seals, all 1st Order Markov estimates of the entropy (\hat{H}_1) lie below the one-tailed 0.95 confidence region of bootstrapped i.i.d. sequence entropy (\hat{H}_0) for the hypothesis that $\hat{H}_0 \leq \hat{H}_1$, which supports the conclusion that $\hat{H}_1 < \hat{H}_0$ with a significant of $p < 0.05$ (Fig. 3(a)). This implies that the leopard seal songs do have time structure, and that knowing the preceding sound in the sequence reduces uncertainty in predicting the next sound. This indicates that the i.i.d. model does not capture the structure of the leopard seal calling bouts.

The lack of a bias correction for the SWML entropy estimates limits the accuracy of these estimates. The SWML estimator is known to contain a positive bias which decreases with increasing window size⁵³ and thus we can assume that all SWML entropy estimates (including the 95% CI for the bootstrapped sequences in Fig. 3(b)) would be reduced when corrected for this bias. However, since we cannot account for this analytically, we only present a conservative estimate of significance. For 21 of the 26 leopard seals, \hat{H}_{SWML} lies below the one-tailed 0.95 confidence region for the hypothesis that $\hat{H}_1 \leq \hat{H}_{SWML}$, thus for these leopard seals we can reject the null hypothesis and infer that the structure of the calls is not fully described by a 1st order Markov model.

The only mammal species for which a SWML entropy estimate has been reported (alongside i.i.d. and 1st order Markov estimates) are humpback whales, with entropy estimates of 0.19–0.79^{54,55}. Mean 1st order Markov estimates have been reported for bottlenose dolphins (with both whistles at 1.15 bits¹⁷ and 'bray' calls at 1.5 bits¹⁸) and squirrel monkeys at 1.23 bits¹¹ which we have compared to the leopard seal entropy estimates (Fig. 4). Direct comparison between leopard seal entropy estimates and those of the bottlenose dolphins and squirrel monkeys is made challenging due to sample size limitations and the lack of bias correction^{11,17,18}. The negative bias inherent to both the i.i.d. and Markov models suggests that the true entropy values are higher than the mean values presented.

When we compare leopard seals with their musical human counterparts (compared specifically to the progression of musical notes in the melody), the entropy estimates of leopard seal songs are higher than those of simple nursery rhymes, indicating they have more randomness. For nursery rhymes, the 39 tunes selected from 'The Golden Song Book' by Katherine Tyler Wessells were found to have a mean entropy estimate (modelled as an i.i.d.) of 0.821⁵⁶, within the lower range of the leopard seal estimates (Fig. 4). While the nursery rhymes were not explicitly calculated as the 1st order Markov model entropies, these values are expected to be significantly lower⁵⁴. In contrast, the leopard seal calling bouts are more structurally constrained and predictable compared to the music by the Beatles⁴³ which ranged from 2.128 to 3.319 bits. They are further constrained still when compared to the best entropy estimates for music by Classical composers (including Hasse, Mozart, Schubert, Hadyn and Mendelssohn) at 3.03 to 4.84 bits^{42,45}. Baroque composers (including Bach, Corelli, Handel and Telemann) at 3.68 to 4.19 bits⁴² and Romantic composers (including Strauss and Schumann) at 3.050 to 3.397 bits^{45,55} (Fig. 4).

ID	t	<i>l</i>	$\hat{\mathcal{A}}$	H_{\max}	\hat{H}_0	\hat{H}_0 (BC)	\hat{H}_1	\hat{H}_1 (BC)	$\hat{H}_{SWML}(n)$	ρ_o	ρ_1	ρ_{SWML}
92 A	90	224	4	2	1.58	1.59	0.68	0.72	0.63 (12)	0.21	0.64	0.68
92B	135	419	6	2.58	2.25	2.26	1.38	1.43	1.38 (16)	0.13	0.45	0.46
92D	135	467	6	2.58	2.13	2.14	0.97	1.01	0.87 (50)	0.17	0.61	0.66
92G	180	537	6	2.58	2.12	2.12	0.96	1.00	0.80 (44)	0.18	0.61	0.69
92 H	90	254	6	2.58	2.26	2.28	1.07	1.15	1.05 (27)	0.12	0.55	0.59
92I	360	833	6	2.58	2.24	2.24	1.17	1.20	1.04 (38)	0.13	0.54	0.60
92P	360	1183	6	2.58	2.13	2.14	0.98	1.00	0.81 (50)	0.17	0.61	0.69
93 A	45	169	5	2.32	1.58	1.60	0.82	0.91	0.75 (28)	0.31	0.61	0.68
93T	45	151	6	2.58	2.02	2.05	1.13	1.28	1.34 (48)	0.21	0.51	0.48
U11	90	230	6	2.58	2.36	2.38	1.27	1.36	0.88 (41)	0.08	0.47	0.66
U13	90	255	6	2.58	2.17	2.19	1.00	1.09	0.98 (49)	0.15	0.58	0.62
U14	90	222	6	2.58	1.96	1.97	0.91	1.01	0.85 (45)	0.24	0.61	0.67
U2	45	416	6	2.58	2.24	2.25	1.38	1.43	1.37 (16)	0.13	0.45	0.47
U20	45	163	6	2.58	2.08	2.10	1.17	1.30	1.25 (17)	0.19	0.50	0.51
U24	90	177	6	2.58	2.08	2.10	0.85	0.97	0.82 (46)	0.19	0.62	0.68
U25	90	238	6	2.58	2.05	2.06	1.05	1.14	1.01 (50)	0.20	0.56	0.61
U26	90	250	6	2.58	2.07	2.08	1.09	1.17	1.04 (46)	0.19	0.55	0.60
U30	90	160	6	2.58	2.36	2.38	1.21	1.34	1.33 (44)	0.08	0.48	0.49
U31	45	381	6	2.58	1.87	1.88	1.09	1.15	0.93 (37)	0.27	0.55	0.64
U32	45	323	5	2.32	1.89	1.90	0.92	0.96	0.65 (50)	0.18	0.59	0.72
U4	135	313	6	2.58	2.22	2.32	1.10	1.17	0.83 (49)	0.14	0.55	0.68
U7	450	946	6	2.58	2.22	2.22	1.24	1.26	1.24 (50)	0.14	0.51	0.52
U79	90	303	6	2.58	2.05	2.06	0.89	0.96	0.75 (26)	0.20	0.63	0.71
U81	270	709	6	2.58	2.03	2.03	0.95	0.98	0.77 (49)	0.21	0.62	0.70
U82	360	706	6	2.58	2.14	2.14	1.12	1.15	1.06 (48)	0.17	0.56	0.59
U9	180	407	6	2.58	2.25	2.26	0.95	1.00	0.89 (34)	0.13	0.61	0.66

Table 1. Male Leopard seal song parameters and modelled estimates of song entropy. The recording length T (min), length of the observed sample calling sequence *l*, observed alphabet size \mathcal{A} , entropy estimations (maximum, i.i.d. (with bias correction), 1st order Markov (with bias correction) and SWML (with window size and bias correction)) and redundancy ρ for each estimator are recorded for each individual seal.

The best entropy estimate values (SWML) are higher in the leopard seal song than those of the humpback whale song (Fig. 4) suggesting there could be more information within the temporal structure of the leopard seal sequences. For the humpback whales, information such as individual identity⁵⁷ or advertisements of fitness⁵⁸ could be conveyed through different means such as frequency and temporal characteristics⁵⁸ or the repetition of motifs⁵⁷ but the structure of the song is more predictable^{53,56}. Kershenbaum et al. suggest that information can be encoded in sequences through six paradigms: repetition, diversity, combination, ordering, overlapping and timing⁵⁹. For leopard seals, the entropy estimates suggest that the structure itself is crucial for conveying information, i.e. that ordering is the method by which information is conveyed. This is consistent with the notion that stereotyped calls are better suited for long distance communication amongst a widely dispersed population, as the characteristics are less likely to be lost due to signal degradation, frequency selective fading or Doppler shift²³.

Change in entropy can be normalised relative to the alphabet size through an estimation of redundancy. Redundancy estimates were calculated from each of the three estimates of entropy for each leopard seal (Fig. 5). The highest estimates of redundancy, typically resulting from the SWML entropy estimate, ranged between 0.51 and 0.72 per song^{52,53}. This is lower than that of humpback whales, which range from 0.81 to 0.96 per song^{53,56}. This indicates that the leopard seals vocalisations, while strongly constrained, are less structurally constrained than the humpback whales.

Recording lengths of the leopard seal calling bouts ranged from 151 to 1183 units, and we used a linear regression to test whether the length of the calling bout had an impact on the estimate of entropy. Data was normally distributed and there was no evidence of heteroscedasticity. We found that the recording length (sequence length) had no influence entropy estimate (linear regression, $p=0.914$, R-squared=0.000498, Fig. 3). From this result we can infer that the recording length limits we imposed (discarding all recordings < 150 units in length) were sufficient to provide confidence in our estimates of the leopard's seal vocalisation entropy.

Vocal behaviour varies amongst size classes of male leopard seals during the breeding season. For the smaller and potentially less fit males, the further along in the season they are, the fewer calls their sequences may contain, due most likely to the fatigue associated with this behaviour²⁸. In contrast, the larger males maintain a more consistent call rate that does not vary throughout the breeding season²⁸. Future studies would benefit from examining this relationship with a larger sample size.

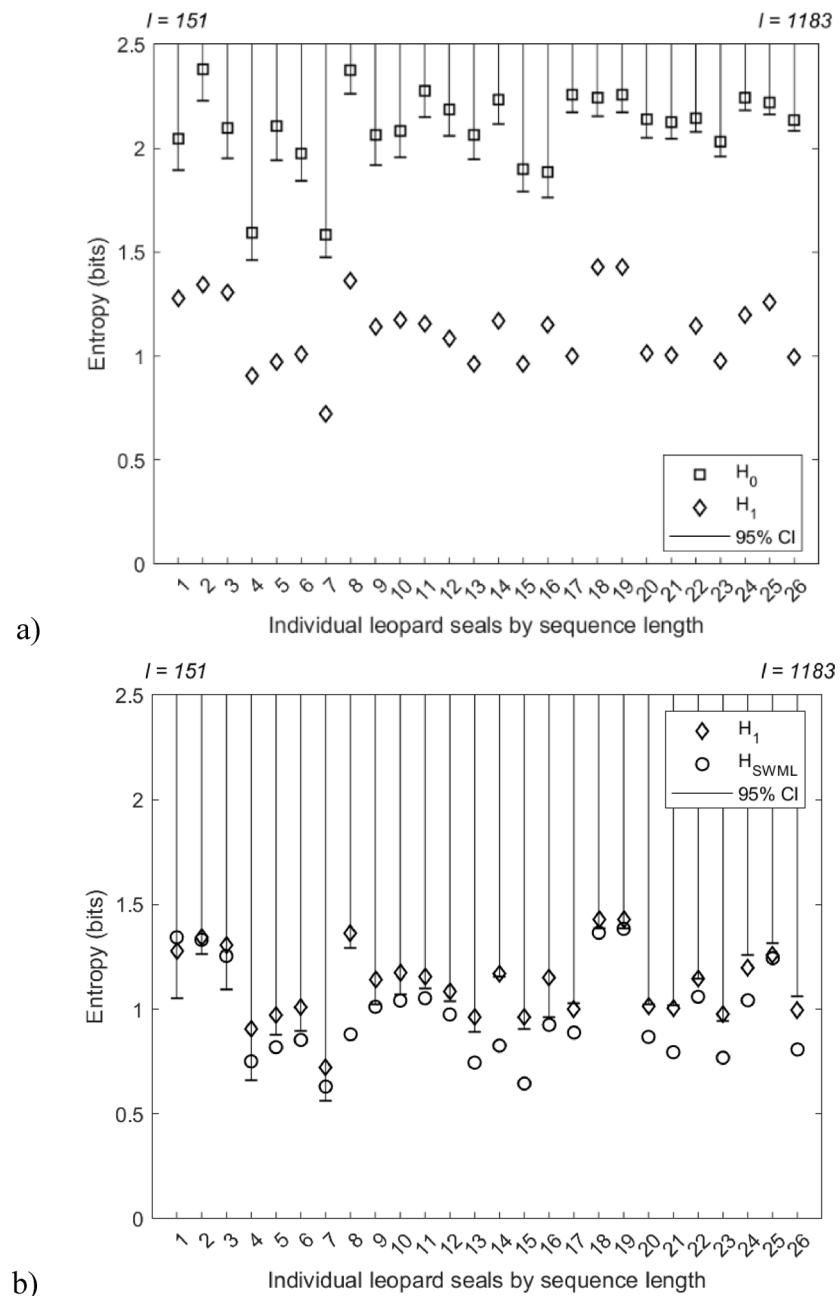


Fig. 3. Results of bootstrapping analysis: (a) the first hypothesis test comparing the i.i.d. to the 1st Order Markov model and (b) the second hypothesis test comparing the 1st Order Markov to the SWML entropy estimates. The horizontal bars indicate the lower bound of the 95% confidence interval for the bootstrapped sequence entropy estimates. Leopard seals are numbered from 1 to 26 in order of the length of their call sequences, ranging from 151 to 1183 units.

Conclusion

Leopard seal song remains an enigmatic behaviour, but by examining the structure of the sequences we can shed light on the means by which information is encoded. From the estimates of entropy, we can infer that the leopard seal calling bouts have more sequential structure than can be fully captured by a 1st order Markov model. While the exact purpose of the leopard seal's singing behaviour is unknown, there is a significant relationship between the typical vocal behaviour of a phocid seal and the nature of its mating system^{23,60}. Pinniped species that breed at higher densities have more calls in their vocal repertoire than those that breed at low densities²³ which could mean that structure plays a more significant role in advertisements of fitness or individual identity for leopard seals as their vocal repertoire contains fewer calls. Similarly, song fulfills a variety of biological functions across many mammalian taxa, including humans. Comparing the leopard seal entropy estimates to other mammalian song systems (including human music) allows us to make inferences on the behavioural significance of sequence

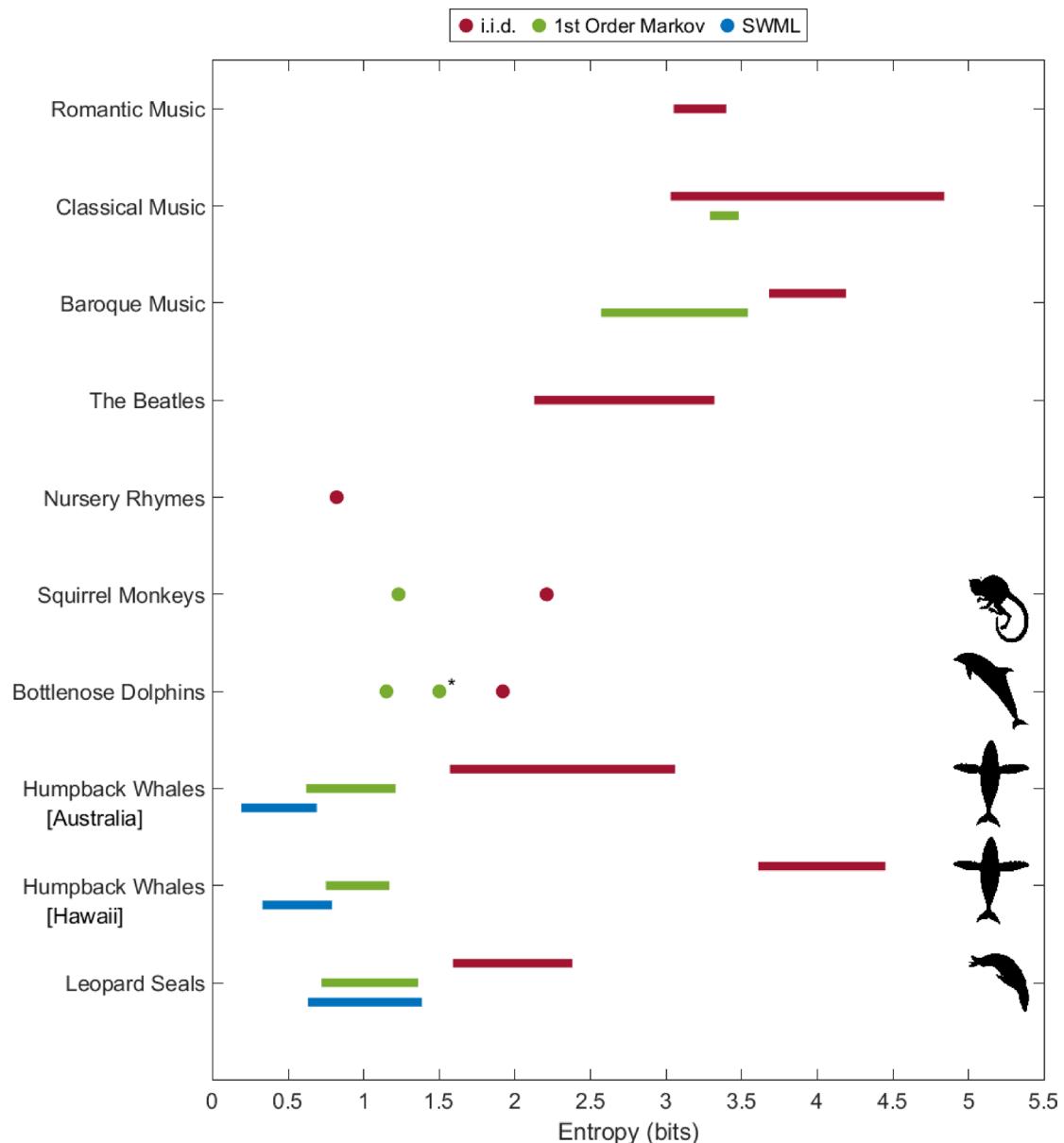


Fig. 4. Comparison of entropy estimates of the Eastern Antarctic male leopard seals with that of the humpback whales (Hawaiian⁵³ and Australian⁵⁶), bottlenose dolphins^{17,18} ('bray' call estimate indicated by *) and squirrel monkeys¹¹ and entropy estimates of melodic contour of various music styles (songs by the Beatles⁴³ various Classical^{42,45} Baroque⁴² and Romantic^{45,55} composers, and children's nursery rhymes⁵⁴). Entropy estimation methods are indicated by colour.

structure. The entropy estimates of the leopard seals being higher than those of the humpback whale suggests that there is comparatively less predictability within the leopard seal sequences, and as such more information is encoded in the structure of the sequences. From this we can infer that structure is necessary for the leopard seals to convey information over long distances, as it is less susceptible to degradation than other acoustic characteristics. This is consistent with previous observations of signalling identity in leopard seals vocal sequences³¹.

Using sequence structure to communicate information about the caller's identity has been observed in other marine mammals - individual identity is coded into some acoustic coda sequences of sperm whales⁶¹⁻⁶³. Individual leopard seals were observed to retain their particular sequences over three days³¹ which suggests that the sequences are stable and could encode information about the singer's identity. The presence of individual identity coding within leopard seal calling sequences should be investigated in future. While the probability laws which govern the pattern of these acoustic sequences are unknowable to us, by modelling the sequence we can gain valuable insight into the acoustic behaviour of leopard seals.

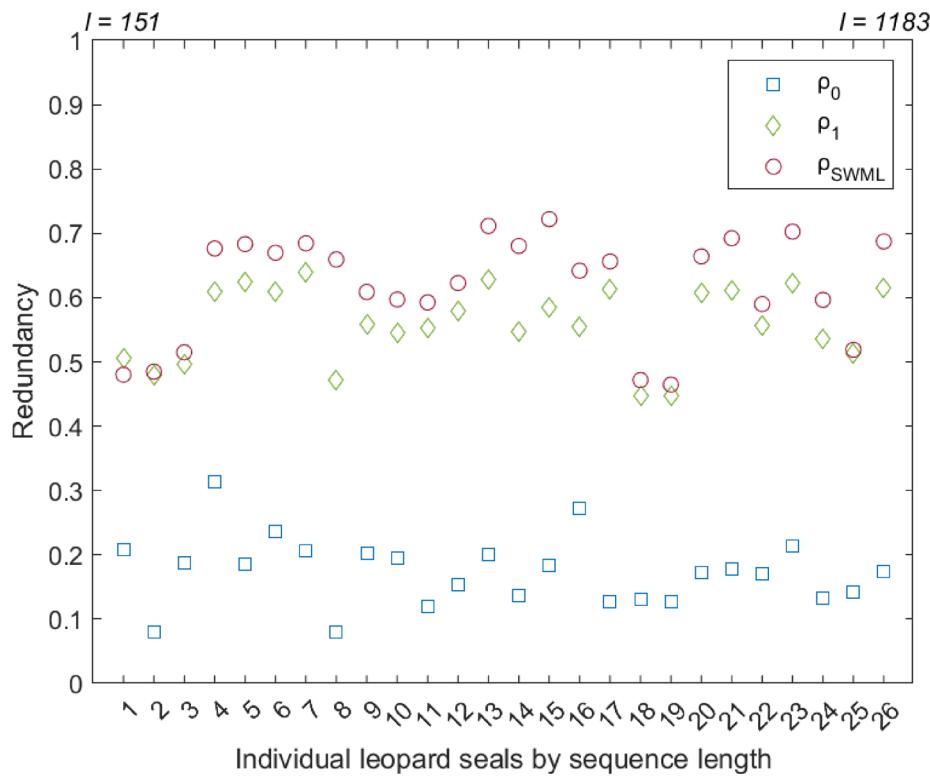


Fig. 5. Comparison of estimates of redundancy from three entropy estimators (i.i.d., 1st Order Markov and SWML) for each individual leopard seal by sequence length.

Methods

Study area and data collection

Recordings were made from November to January in 1992 to 1994 and 1997 to 1998, in the Davis Sea, Eastern Antarctica (from $68^{\circ} 25' S$, $77^{\circ} 10' E$ to $68^{\circ} 35' S$, $77^{\circ} 50' E$). The recordings were made between 1600 and 0300 along the edge of the fast ice, to correspond with the period of highest vocal activity^{21,31}. Recordings were made on 45-minute tapes with a Sony WMD6C audio-cassette recorder, a Brüel and Kjær 8103 hydrophone and a custom preamplifier, and this system had a frequency response from 35 to 15 000 Hz ± 3 dB. The hydrophone was deployed 6 m below the surface of the water. Individual seals were identified with an oil-based paint in distinctive patterns to maximise the likelihood of recording the same seal. Calls were grouped by month (November, December or January).

Call classification

Recordings were excluded when two animals were observed to be calling simultaneously or when the signal-to-noise ratio (SNR) was too low. Terminology often varies across taxa, as such in this study we define a 'call' to be a single sound unit, a 'calling bout' to be an unbroken string of calls delivered underwater between successive returns to the surface, and a 'song' to be a session of successive calling bouts. The discrete call types used in this analysis were identified in Rogers et al., 1995. Five distinct call types were identified in these recordings and annotated with the following symbol: high double trills (H), medium single trills (M), low descending trills (D), low double trills (L) and a hoot with a low single trill (O). This classification is consistent with the systems defined in^{20,31}. A break between calling bouts, identified by a period of silence between bouts, was marked with a 'Z' in the sequence. Spectrograms of calls were produced using Visualization Software (LLC version 16.0) with a 4096 point fast Fourier Transform, 75% overlap, 50 s window, yielding 15.625 Hz frequency resolution. Calls were classified manually by a single observer and then checked by a second blind observer. To avoid pseudo-replication, only one recording of underwater vocalisations by each individual seal was included in the analysis. If the vocalising leopard seal's identity was unknown (either because the seal had not been marked or because the seal had moved into the water prior to the arrival of the research team), the sequences were compared with those in Rogers and Cato 2002³¹ to eliminate recordings of the same individuals.

Entropy analysis

This entropy analysis method is derived from the method detailed in Suzuki et al., 2006. The leopard seals can be considered an information source (or process) \mathcal{X} which produces a sequence of outputs dictated by the source's probability law. If X_i is a random variable representing the source output at time i , where X_i^j denotes $(X_i, X_{i+1}, \dots, X_j)$, $i \leq j$, then a particular sample output (i.e. vocalising bout) of the random variable is denoted by x_i^j . The probability distribution $Pr\{X = x\}$ is denoted by $p(x)$. The source can be

considered to be stationary if all joint probability distributions are time invariant and can be considered ergodic when all outputs possess the same statistical properties. The Shannon entropy of a source can be calculated directly from the probability distribution of the source. However, since the true probability distribution of a vocalising animal is unknown, the entropy can be estimated by assuming a model distribution. The entropy of a sequence is maximised when all outcomes are equally likely. For example, a fair die has higher entropy or ‘randomness’ than a biased die, which is more predictable and thus lower entropy. Assuming that all of the sounds an animal can produce are equally likely creates an estimate of the maximum entropy.

The first model is the independent identically distributed (i.i.d.) model, which assumes that there is no time structure to the source (i.e. each output has no dependence on previous outputs). To calculate the empirical distribution from a sample sequence x'_1 of length l , the probability of each output is calculated as:

$$\hat{p}(a) = \frac{|\{i : x_i = a, i \in [1, l]\}|}{l} \quad (1)$$

Where the estimated alphabet $\hat{\mathcal{A}}$ is

$$\hat{\mathcal{A}} = \{i : x_i \in [1, l]\} \quad (2)$$

The entropy can then be estimated as

$$\hat{H}_0 = - \sum_{a \in \hat{\mathcal{A}}} \hat{p}(a) \log_2 \hat{p}(a) \quad (3)$$

The second model estimated is a first order Markov model, which assumes that each output is dependant only on the output that immediately preceded it. The empirical joint and conditional probabilities of each pair of possible outputs are calculated from the observed sample sequence.

$$\hat{p}(a_1, a_2) = \frac{|\{i : x_{i-1} = a_1, x_i = a_2, i \in [2, l]\}|}{l - 1} \quad (4)$$

$$\hat{p}(a_1 | a_2) = \frac{|\{i : x_{i-1} = a_1, x_i = a_2, i \in [2, l]\}|}{|\{i : x_i = a_1, i \in [2, l]\}|} \quad (5)$$

The entropy estimate can then be calculated as

$$\hat{H}_1 = - \sum_{a_1, a_2 \in \hat{\mathcal{A}}} \hat{p}(a_1, a_2) \log_2 \hat{p}(a_1 | a_2) = - \sum_{a_1, a_2 \in \hat{\mathcal{A}}} \hat{p}(a_1, a_2) \log_2 \hat{p}(a_1, a_2) - \hat{H}_0 \quad (6)$$

This concept can be similarly extended for higher order Markov models, i.e. an n th order Markov model assumes that the output is dependent on the previous n symbols³⁸. As the alphabet of the seals consisted of a maximum of 6 symbols³⁰ there are 36 theoretical transitions that are possible within the sequences. The data must be sufficiently long enough to obtain accurate estimates of the probabilities in Eqs. (4) and (5), and thus a minimum sequence length of $10 \times 36 = 360$ units would be appropriate to calculate an empirical probability distribution. However, in practise we observe significantly less transitions (e.g., two consecutive “Z” symbols are impossible in the sequence as a “Z” indicates a period of unlimited silence), and as such we set the minimum sequence length to be 150 symbols and discarded any sequences below this length. Higher order Markov estimates were not calculated due to these sample size constraints.

The third entropy estimator used in this study was a model-free non-parametric entropy estimator, the Sliding Window Match Length (SWML) entropy estimation. This entropy estimate is desirable as it is applicable to a broader class of sources and converges rapidly in sequence length l , meaning that it produces a good estimate of the entropy from a relatively short sequence of data. Wyner and Ziv calculate the SWML entropy estimate for a stationary ergodic source with vanishing memory as:

$$\frac{E[L_i(n)]}{n} = \frac{1}{H} + \frac{O(1)}{\log n} \quad (7)$$

Where n is equal to the width of the sliding window⁶⁴. For a window size n and a sequence index i , the match length $L_i(n)$ is defined as

$$L_i(n) = \max \{L : x_i^{i+L-1} = x_{i-k}^{i-k+L-1}, k \in [1, n]\} \quad (8)$$

For a window of size n immediately preceding a symbol x_i in the observed sequence at index i , the match length is the longest string of symbols inside the window which matches the symbols following x_i . The match length is related to the source entropy via the following Eq.

$$\lim_{n \rightarrow \infty} \frac{L_i(n)}{\log n} = \frac{1}{H} \text{ with probability one.} \quad (9)$$

The SWML entropy estimator for a stationary ergodic process is defined as follows, where n is the specified fixed window size and n'_i is the effective window size (defined as such to remove errors in edge cases when $i < n$).

$$\hat{H}_{SWML}(n) = l \left[\sum_{i=3}^l \frac{L_i(n'_i)}{\log n'_i} \right]^{-1} \quad (10)$$

where

$$n'_i = \min \{i-1, n\}. \quad (11)$$

Even when sequence length requirements are met, both the i.i.d. and Markov models exhibit a negative bias due to Jensen's Inequality^{38,51} and so we have bias corrected the entropy estimates using the Eqs. (12) and (13)⁶⁵.

$$\hat{H}'_0 = \hat{H}_0 + 0.72 \frac{|\hat{\mathcal{A}}| - 1}{l} \quad (12)$$

$$\hat{H}'_1 = \hat{H}_1 + 0.72 \frac{|\hat{\mathcal{D}}| - |\hat{\mathcal{A}}|}{l} \quad (13)$$

With $\hat{\mathcal{A}}$ and l as defined in Eq. (1), and where $\hat{\mathcal{D}}$ is equal to the number of all observed diagram transitions (pairs of symbols). In contrast, the SWML exhibits a positive bias which cannot be analytically accounted for, although it is known to be $\frac{O(1)}{\log n}$, and thus vanishes with increasing window size n ⁵³.

Two hypotheses were tested to determine whether the leopard seal vocalisations contained time structure that was captured by the Markov or SWML entropy estimates. The first hypothesis test compared the entropy estimates from the i.i.d. and 1st Order Markov models against each other, where the null hypothesis was that the source does not have time structure (i.e. knowing the previous symbol does not reduce uncertainty about the current symbol). Thus, the null hypothesis predicts that $\hat{H}_0 = \hat{H}_1$ (significance level $\alpha = 0.05$). The alternate hypothesis is then $\hat{H}_0 > \hat{H}_1$, and this is a one-sided test as further constraining the system cannot increase the uncertainty. Similarly, we compared the 1st order Markov model and the SWML estimate such that the second null hypothesis predicts that $\hat{H}_1 = \hat{H}_{SWML}$, i.e. knowing more than one previous sound in a call sequence does not increase our ability to predict the next sound (thus the alternate hypothesis is $\hat{H}_1 > \hat{H}_{SWML}$).

For each individual leopard seal, an empirical i.i.d. probability distribution was obtained by observing the occurrence of each sound in the call sequence. To establish bootstrap confidence bounds for the first hypothesis test, we simulated a set of 1000 bootstrap i.i.d. call sequences of equal length to each seal's original recorded vocalisation, drawn from the empirical i.i.d. probability distribution. Next, we estimated the first order Markov model entropy for each of the synthetic sequences and calculated a 95% one-sided confidence interval for this dataset. If the 1st order Markov entropy estimates of the leopard seal calling bouts are below this confidence bound, the result is significant, and we can reject the null hypothesis. Similarly, we established the confidence bounds for the second hypothesis test by creating 1000 sequences generated by the empirical first-order Markov model estimated from the sequence after counting all sequential pairs of sounds in each leopard seal calling bout. If the SWML entropy estimate is lower than the confidence bound of the bootstrapped Markov sequences, the first-order Markov model does not capture all of the structure in the sequence. Several studies of animal acoustical communications have compared entropy estimates from different order Markov models^{11,17,18} though only Suzuki et al. and Miksis-Olds et al. applied the SWML estimator to obtain a nonparametric bound on the entropy^{53,56}.

The redundancy of each observed sequence is calculated from the entropy estimates using the Eq. (14).

$$\rho = \frac{H_{\max} - \hat{H}}{H_{\max}} \quad (14)$$

The estimates of redundancy were calculated from the entropy estimator with the consistently lowest estimates of entropy.

Data and code availability

The observational data and the analysis code that support the findings of this study are available in Dryad with the identifier: <http://datadryad.org/share/bz11C1ir9UmWPaviBHZV8SUq5XtXYsDZ1HW055GVbw>. Data will be made publicly available in Dryad upon publication. Annotated leopard seal sequence files are also provided as supplementary information files. Correspondence and requests for materials should be addressed to Lucinda Chambers (lucinda.chambers@unsw.edu.au).

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Author contributions

T.R. recorded the leopard seal vocalisations and annotated the call recordings. J.B. created the analysis methodology. L.C. conducted the entropy analysis, prepared all figures and wrote the main manuscript text. All authors were involved in project conception, manuscript production and revision.

Declarations

Competing interests

The authors declare no competing interests.

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Additional information

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