

Article

Calling underwater is a costly signal: size-related differences in the call rates of Antarctic leopard seals

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Abstract

It is proposed that where sexually selected vocal communication is an honest signal, the call production rate is predicted to change throughout the breeding season. Male leopard seals call underwater for many hours each day over their three- to four-month breeding season, and it is hypothesized that a decrease in calling rate would be associated with the declining body condition of smaller males. The calling rates of leopard seals were measured ($N = 49$ recordings) and compared between seals of different size classes throughout the breeding season. Male leopard seals produce their calls at more stable rates as they become larger. In this study, larger male leopard seals adopted a strategy of consistent underwater calling throughout the breeding season, whereas there was a breakdown in the calling stereotypy of the smaller males at its height. Toward the end of the breeding season, the smaller seals produced fewer calls in shortened calling bouts, and they took more rest periods. Therefore, underwater calling may represent an honest signal in the leopard seal. For marine mammals that call underwater, the production of repetitive sequences advertises the breath-holding ability of the caller to the listeners, and this ability may be related to male stamina and endurance, thus representing an honest signal that could be widespread in other species.

Key words: acoustic cues, costly signaling, display behavior, honest advertisement, marine mammals, vocalizations.

Vocal behavior has the potential to indicate physical condition and could be used by conspecifics as a source of information to assess fitness (Vannoni and McElligott 2009). Thus, if vocal signals are used in sexual selection, they should represent an honest, costly signal. In birds, singing performance is a reliable indicator of an individual's quality (Catchpole 1996), and calling rate is believed to be a costly trait due to increased oxygen consumption and energy expenditure (Catchpole 1996). For mammals that call underwater, there is an additional cost because the caller cannot breathe while vocalizing underwater. Male aquatic-mating pinnipeds produce vocal courtship displays during the breeding season (Rogers 2003, 2005; Stirling and Thomas 2003; Van Parijs 2003), and these underwater vocalizations are frequently associated with dive displays that are likely associated with male competition and mate attraction (Rogers

et al. 1996; Rogers 2003, 2005; Van Parijs 2003). If the underwater calling and diving behavior of marine mammals represents costly signaling, a change in the call production rate would be anticipated as the breeding season progresses.

For a mammal calling underwater, calls produced in rapid succession could indicate that the caller has not had time to surface to take a breath; therefore, the ability to produce long vocalization sequences over prolonged periods could advertise the breath-holding ability of the caller. Producing rhythmically repeated patterns of vocalizations may advertise acoustic endurance and be a measure of the fitness of the male caller, that is, an indication of breath-holding stamina. Stereotypic, rhythmic signaling has been documented in several marine species, including pinnipeds such as in the bearded seal *Erignathus barbatus* (Van Parijs et al. 2001), the harbor seal

Phoca vitulina (Van Parijs et al. 1999), the walrus *Odobenus rosmarus* (Stirling et al. 1987; Verboom and Kastelein 1995), and the leopard seal *Hydrurga leptonyx* (Rogers and Cato 2002), as well as cetaceans including humpback *Megaptera novaeangliae*, fin *Balaenoptera physalus* and blue *Balaenoptera musculus* whales (Ljungblad et al. 1982; Herman and Pack 2003; Tripovich et al. 2015).

Animals that are distributed at low densities in the marine environment can face challenges in communicating with one another. As sound propagates through water over long distances, the signal becomes degraded due to frequency-dependent transmission or interference (i.e., from multi-path propagation; Urlick 1983), which may corrupt the information contained within the original signal. The repetition of a few stereotyped vocalizations could enhance call recognition in a distant receiver, particularly where the signal-to-noise ratio is poor, which is common when individuals are spaced at significant distances from one another (Rogers 2003, 2005; Van Parijs 2003).

To overcome long-range communication challenges, widely distributed marine animals tend to produce highly stereotyped calls that are repeated in sequences. Repetitive vocal display behavior may have evolved to counteract the loss of information during transmission, or it may have developed as an adaptation to noisy environments (Terhune and Ronald 1986; Lengagne et al. 1999; McElligott and Hyden 1999; Rogers and Cato 2002; Moors and Terhune 2004; Brumm and Slater 2006). In the production of a repetitive vocal display, not altering the calling rate may provide an advantage in long-distance signaling.

Leopard seals are distributed at low densities throughout the Antarctic pack ice (Southwell et al. 2008; Forcada et al. 2012; Rogers et al. 2013), and male leopard seals vocalize underwater for many hours each day during the breeding season, producing a few stereotyped calls that are repeated in patterns (Rogers and Cato 2002; Rogers 2007). Male leopard seals in the wild begin calling underwater at the start of the breeding and mating season (Rogers 2009), and both captive male and female seals call when their reproductive hormones are elevated (Rogers et al. 1996). Vocalizing likely plays a role in mate attraction as well as male–male territorial signaling, and whether aiding in female mate choice or male–male territoriality, it would play a role in intraspecific assessment and is presumably energetically expensive.

As male leopard seals cannot breathe while underwater, calling may advertise the breath-holding ability of the caller to potential listeners. Male seals repeat an alternating calling-resting-calling pattern underwater over periods of approximately 2 min, between which they return to the surface of the water for periods of one to one and a half minutes, during which time they do not vocalize (Rogers 2007). The calls of male leopard seals are loud (i.e., up to 177 dB re 1 μ Pa at 1 m, Rogers 2014), and individuals call underwater during these dive cycles for many hours each day throughout their three- to four-month breeding season (Rogers 2007). Leopard seals typically dive to shallow depths (i.e., 30 m or less; Krause et al. 2015), and while calling, each vocalizing bout consists of 8–12 calls produced in stereotyped sequences that carry individually distinctive information (Rogers and Cato 2002). These vocalizing bouts potentially identify the breath-holding capacity of the caller while underwater based on the period of silence during the inter-vocalizing periods, that is, the time required at the surface of the water between bouts. Breath holding may be related to the stamina and endurance of male seals and thus represents an honest signal.

In the Davis Sea of eastern Antarctica, leopard seals produce five types of calls (Rogers et al. 1995; Rogers 2007). These calls are

produced in a specific order, which represents a first-order Markov relationship; successive calls in a sequence can be predicted based on the preceding call (Rogers and Cato 2002). This means that the calls are produced in similar proportions relative to one another, which should promote consistency rather than variability in call production. For seals to retain these individually distinctive sequences, it is predicted that they must maintain a constant number of calling periods (vocalizing bouts) and rest periods between bouts (inter-vocalizing periods) as well as a constant calling rate of the five call types through the breeding season.

Seasonal rate changes

The availability of mating opportunities and the intensity of competition between male leopard seals changes through the breeding season. Although female leopard seals are asynchronous in their estrus, the number of sexually receptive females is greatest in December (Southwell et al. 2003). Female leopard seals that have had a pup will enter estrus and become sexually receptive once they have weaned that pup. Pupping can occur at any time during the austral summer.

In the eastern Antarctic, leopard seal female–pup pairs can be observed hauled out on ice floes from early November onwards (Southwell et al. 2003), and the lactation period is likely to be greater than 24 days (Southwell et al. 2003). Therefore, a decline in female–pup pairs on the pack ice in early December reflects the commencement of the weaning of pups born early in the season and the commencement of estrus in mature females. As pupping time is asynchronous, pups will continue to be weaned and females in estrus will continue to become available through December. However, female leopard seals that do not pup in a given year can become sexually receptive as early as October (Southwell et al. 2003). Male leopard seals commence calling underwater in late October and continue through to the beginning of January (Van Opzeeland et al. 2010), and the peak in mating is likely December when the availability of sexually receptive females is highest. Female–pup pairs are absent in January, so this is the time when estrus females are no longer available. In the Weddell Sea, leopard seal calling peaks in December (Van Opzeeland et al. 2010).

Changes in calling rate, with an increase from the beginning of the breeding season to the peak, have been reported in many vocalizing species (Van Parijs 2003; Vannoni and McElligott 2009), including the leopard seal (Van Opzeeland et al. 2010), and such an increase in signaling prior to the peak could be a source of information for intrasexual assessment to aid in female mate choice (Vannoni and McElligott 2009). However, for long-distance communicators such as the leopard seal that call in stereotyped sequences, calling at a constant rate would seem more advantageous.

It is predicted that the calling rate of male leopard seals should remain stable throughout the breeding season because males cannot predict where or when sexually receptive females can be accessed over the breeding season; the calls of males travel over great distances, and calling dive displays are performed over long periods. Stereotyped calling behavior would counter signal degradation due to long-range propagation and signal masking by background noise. In addition, the males would need to produce the same mean number of calls per vocalizing bout to retain their individual sequences.

Size-related differences

Physiological and social factors change during the breeding season and can have a strong effect on the males and, in turn, on the rate at

which they produce call (Vannoni and McElligott 2009). If the underwater calling behavior of the leopard seal represents an honest signal, it is anticipated that a change in the call production rate throughout the breeding season would be observed in less fit individuals. A sustained underwater vocal performance by superior males would advertise their greater fitness as they would appear not to have become fatigued during the breeding season. However, smaller and potentially less fit males may become fatigued through the breeding season; therefore, vocal signaling in these seals would vary over time in response to the changing intersexual and intrasexual selective environment.

There are size-related differences in the acoustic features of calls produced by male leopard seals (Rogers 2007). The acoustic signals of land mammals tend to be driven by their body size, typically the larger an animal's size, the lower frequency vocalization it can produce (Fitch, 2000; Martin et al. 2016). Aquatic mammals appear released from this scaling rule (Martin et al. 2016), the leopard seal for example produces calls of higher frequencies (i.e., up to 4,800 Hz; Rogers et al. 1995) than anticipated for its large body size (i.e., up to 500 kg, Van den Hoff et al. 2005; Rogers 2009). As leopard seals mature, they produce calls of higher fundamental frequencies, large male leopard seals produce particular calls at higher frequencies than smaller males (Rogers 2007). This trait has been documented in other large mammals such as the red deer *Cervus elaphus* (Reby and McComb 2003).

If calling underwater is a costly signal that communicates fitness information to conspecifics, it is hypothesized that larger male leopard seals would maintain a consistent calling rate throughout the breeding season, whereas later in the breeding season, smaller males would: (1) take more rest (inter-vocalizing) periods than the larger seals and thus engage in more vocalizing bouts; (2) produce a fewer mean number of calls within these shorter vocalizing bouts and thus a smaller number of calls overall; and (3) reduce the number of the more commonly heard calls to produce shorter vocalizing bouts.

Materials and Methods

Underwater acoustic recordings

One hundred and eighty-three underwater acoustic recordings of vocalizing male leopard seals were made in 1992 and 1993 along 45 km of the fast ice between 68°25' S, 77°10' E and 68°35' S, 77°50' E in Prydz Bay in the Davis Sea, eastern Antarctica. The leopard seals were confined to ice floes at the very outer edge of the fast ice. A hydrophone (a calibrated Brüel and Kjær 8103) was placed between 5.5 and 6 m below the water surface and 4 m below the under-surface of the fast ice and connected to a custom preamplifier and a Sony WMD6C digital audio recorder (DAT). The system had a frequency response between 35 and 15,000 Hz \pm 3 dB, which was well within the range of the calls (Rogers et al. 1995; Rogers 2007). Only recordings with at least 30 min of uninterrupted, consecutive calls from the same individual were used.

To identify the location of the leopard seals, aerial surveys were conducted at midday, which is the time when leopard seals are most likely to be hauled out on the ice (Rogers and Bryden 1997). While hauled out on the ice, the seals were approached on foot; they were not sedated because of the high mortality risk from anesthetic-related complications (Higgins et al. 2002). The seals were identified as male by the presence of a genital slit and as female by the presence of teats. The fur of the seals was marked in individually distinctive patterns with a non-toxic, oil-based paint, which was observed to

remain on the fur until January of the following year. No long-term adverse effects were observed from this procedure, and Animal Ethics and other relevant permits were obtained from the Antarctic Science Advisory Committee (ASAC) under program number 1144.

Underwater recordings were made at sites where male leopard seals had been observed hauled out on the ice. Underwater acoustic recordings were made while a seal was still asleep on the ice and then after it entered the water. A recording was determined to have been produced by an individual marked seal if (1) no other leopard seals were vocalizing nearby prior to the seal entering the water and (2) vocalizing commenced within 5 min of the seal entering the water. It was difficult to record the underwater sounds of a large number of known individuals as the seals moved out to sea, away from the recording site, before vocalizing commenced, or if they did not vocalize.

Forty nine of the 183 30-min underwater acoustic recordings were of vocalizations by different individuals (Table 1). To reduce pseudo-replication, only one recording of underwater vocalizations by each individual seal was included, and if the identity of the vocalizing seal 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, a comparison of the individually distinctive call sequences within vocalizing bouts (Rogers and Cato 2002) was used to eliminate recordings of the same individuals.

Size class of the seals

In an earlier study, that showed that larger male leopard seals produce particular calls at higher frequencies than smaller seals (Rogers 2007), the leopard seals had been categorized into "age-classes" based on their size. Here, in this study, the seals size alone is used rather than the earlier "age-class" terminology. This is because subsequent research, which followed tagged leopard seals, revealed that smaller seals are not necessarily sexually immature sub-adults (Rogers TL, unpublished data). The size of the seals was estimated while they were hauled out and was based on their length; and as we had not sedated the seals it was not possible to measure the measure standard length (i.e., the linear distance from the tip of the nose to the tail which is the typical measure for phocid seals). The seals that were less than 290 cm in total length (i.e., nose to the end of the hind flippers) which equates to a standard length of 255 cm in this population (Rogers TL, unpublished data), were categorized as small, while seals greater than 290 cm were categorized as large. Sixteen of the 49 recordings of the underwater vocalizations of male leopard seals were made from seals that had been observed hauled out on the ice; thus, a size class had been assigned to those recordings based on the seals' observed characteristics (Table 1). For the 33 recordings for which the seal had not been observed so that the size class was unknown, acoustic characteristics were used as a proxy to ascribe a size class to the seals. Within the study area, male leopard seals produce two calls whose acoustic characteristics exhibit size-related differences: the low double trill (L; Figure 1A) and the high double trill (H; Figure 1B) (Rogers 2007). The size of the calling seal was predicted using the average center frequency of the L call, which is greater than 315 Hz for larger seals and below 315 Hz for smaller seals. Where there was ambiguity, that is, where the average center frequency of the L call was \sim 315 Hz, the average center frequency of the of H call was used; a call above 2680 Hz was assigned to a larger seal while one below this frequency was assigned to a smaller seal. Of the 49 recordings 24 were vocalizations assigned to large seals and 25 of small seals (Table 1).

Table 1. Recording metadata

Seal size	Recording date	Recording time (local)	Number of vocalizing bouts	Number of inter-vocalizing periods	Mean number calls per bout	L	H	O	D	M
Large ^a	16 November 1992	19:15	10	10	7	38	37	3	0	0
Small ^a	16 November 1992		7	8	9	31	31	5	0	0
Small ^b	17 November 1992	14:15	8	8	17	43	44	17	4	24
Large ^b	25 November 1992		11	11	10	38	40	8	3	9
Small ^b	25 November 1992	21:00	8	8	12	34	38	10	4	9
Large ^a	29 November 1992	17:50	11	10	8	30	34	8	4	11
Large ^a	29 November 1992	18:21	10	11	8	28	35	5	4	11
Large ^b	5 December 1992	21:00	13	14	6	31	31	2	6	6
Large ^b	5 December 1992	23:20	7	8	11	30	32	5	3	5
Small ^{1b}	5 December 1992	2:00	8	9	23	31	33	9	6	18
Large ^b	7 December 1992	16:40	8	9	7	22	19	5	4	8
Large ^b	7 December 1992	18:15	8	9	8	28	22	7	2	8
Large ^b	7 December 1992	19:55	8	9	7	24	20	4	3	6
Large ^b	7 December 1992	21:55	6	7	10	27	21	5	4	10
Large ^b	7 December 1992	22:11	10	10	6	27	21	1	3	11
Large ^a	8 December 1992	2:13	11	12	6	21	24	7	3	9
Small ^{2a}	8 December 1992	3:50	10	10	7	29	29	4	2	7
Small ^a	8 December 1992	4:43	11	12	8	32	32	4	3	8
Large ^a	8 December 1992	7:53	9	10	10	30	33	1	5	12
Large ^a	8 December 1992		13	13	6	31	30	6	2	7
Small ^a	8 December 1992	23:40	14	14	4	26	22	2	2	5
Small ^a	9 December 1992	1:20	11	12	5	25	21	3	2	5
Small ^a	9 December 1992	2:55	16	17	3	22	19	1	1	2
Small ^a	9 December 1992	6:55	9	10	7	28	27	1	2	7
Small ^a	11 December 1992	18:15	10	10	9	30	32	7	4	9
Small ^a	11 December 1992	18:55	9	10	7	26	22	4	2	6
Large ^a	12 December 1992	7:45	10	10	10	32	36	7	4	11
Small ^a	17 December 1992	21:45	12	13	5	22	20	8	5	8
Small ^a	26 December 1992	3:00	11	12	6	26	26	2	4	7
Small ^a	4 January 1993	0:10	13	14	5	31	24	3	3	5
Small ^a	6 January 1993	8:20	9	10	7	30	27	5	1	3
Small ^a	9 November 1993	22:00	7	8	12	25	35	10	3	10
Small ^b	12 November 1993	22:30	10	10	13	59	45	7	0	1
Large ^b	13 November 1993	21:45	9	9	11	41	38	7	0	12
Small ^a	15 November 1993	23:20	9	9	11	41	42	7	1	4
Small ^b	18 November 1993	22:00	9	9	15	54	55	12	3	11
Large ^b	21 November 1993	23:20	6	6	15	29	35	3	4	18
Small ^a	25 November 1993	23:45	8	8	9	33	34	4	1	6
Large ^a	26 November 1993	3:00	8	8	9	29	33	4	4	10
Large ^a	27 November 1993	15:00	8	8	7	21	23	3	3	4
Small ^a	27 November 1993	18:20	9	9	9	29	33	33	6	3
Large ^a	3 December 1993	0:00	6	6	12	30	34	3	3	10
Large ^a	4 December 1993	23:00	10	10	10	38	41	8	4	9
Large ^a	4 December 1993	1:00	7	7	13	33	39	8	2	12
Small ^a	5 December 1993	22:00	11	11	8	39	40	5	3	8
Small ^a	5 December 1993	0:00	12	12	5	23	23	2	3	8
Small ^a	6 December 1993		8	8	9	24	29	2	5	7
Large ^a	8 December 1993	1:30	8	8	10	32	33	4	2	5
Large ^b	13 December 1993	2:00	10	10	11	28	30	17	7	9

Notes: Metadata of underwater acoustic recordings of vocalizing male leopard seals ($N=49$) made in Prydz Bay in the Davis Sea, eastern Antarctica. Size of the seals: large 290 cm and small < 290 cm. Recording time is local time, which is UTC/GMT + 7 hours. The number of vocalising bouts, vocalising periods, calls per bout, L, H, O, D, and M calls in 30-min recordings for each seal., ^a Size identified by: prediction using the acoustic characteristics of the calls as a proxy to ascribe the seals' size., ^b Size identified by: from direct observations of the seal.

Seasonal timing

The 49 recordings were made across 51 days of the breeding season in 1992 and 34 days in 1993. In 1992, the recordings were made between 16 November 1992 and 6 January 1993, and those in 1993 were made from 9 November 1993 to 13 December 1993 (Table 1). Recordings were grouped into two time periods, November and December, based on the likelihood of the presence of sexually

receptive females. The November recordings ($N=17$) were made during a period when the availability of sexually receptive females was lower, and this timing was confirmed by a change in the ratio of female-pup pairs to larger lone seals observed within the Antarctic pack ice in the Davis Sea region (Southwell et al. 2003). The December recordings ($N=32$) were made during a period representing the peak of mating opportunities when the availability of

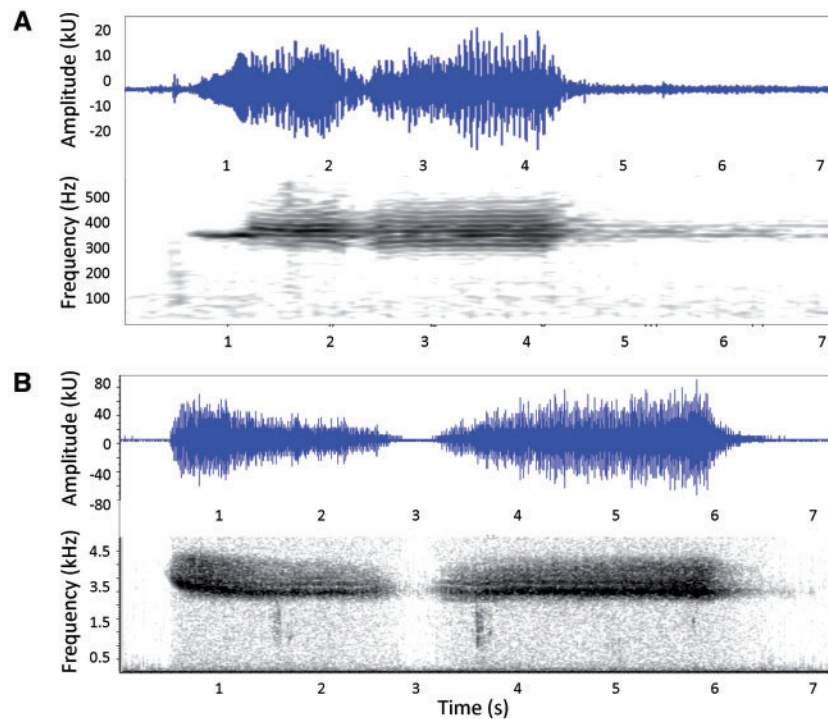


Figure 1. Waveform and sonagram produced in Raven Pro 1.5.0 of leopard seal (A) low double trill (L) sampling rate 44,100 Hz, view range = 0 to 600 Hz, window length = 7 s, and (B) a high double trill (H) sampling rate 11,025 Hz view range = 0 to 5 kHz, window length = 7 s. Spectrograms were generated in Raven Pro v1.5.0 sound editor window (Hann window shape).

sexually receptive females was highest. Two recordings were made in January, and the last male leopard seal was recorded on the 6th of January; these recordings were included in the December category (Table 1).

Calling rate

To reliably estimate the calling rate, we collected our recordings using the all-occurrence sampling technique (Altmann 1974). The type of call within each 30-min recording was counted by two observers using a Spectrogram Version 16.0 (Visualization Software LLC), and counts made by the same observer were used to account for inter-observer differences. The term “vocalizing bout” was used to describe the number of calls produced in a sequence, which was assumed to be produced during the time that a seal spent vocalizing underwater (Rogers and Cato 2002). The term “inter-vocalizing period” was used to describe the period of silence between consecutive vocalizing bouts. Leopard seals in the Davis Sea of eastern Antarctica produce five species-specific calls (Rogers et al. 1995; Rogers 2007): the low descending trill (D); the hoot with a low single trill (O); the medium single trill (M); the H; and the L. The number of vocalizing bouts, inter-vocalizing periods, and each type of leopard seal call was recorded for each 30-min recording.

Data and statistical analysis

Statistical analysis were performed in R (R Core Team 2016), Mixed-effect models fitted with a restricted maximum likelihood with “REML” (lme4 function) were used to investigate the effect of seal size (small or large) and the time during the breeding season (early or late) on the following calling parameters: the number of vocalizing bouts (466 bouts; mean 9.5 ± 0.3 bouts per recording; $N=49$ recordings) and inter-vocalization periods (486 inter-

vocalizing periods; mean 9.9 ± 0.3 per recording; $N=49$ recordings) in 30 min; the mean number of calls per bout (3,778 calls in 466 bouts; mean 9.1 ± 0.5 calls per bout for each recording; $N=49$ recordings); and the variability (SE) in the number of calls per bout (mean 0.8 ± 0.1 SE number of calls per bout per recording; $N=49$ recordings). Additionally, the call rate parameters of each call type were investigated out of 3,778 total calls (mean 77.1 ± 3.0 calls per recording; $N=49$ recordings) as well as rate at which each of the five call types were produced: 149 D calls (3.0 ± 0.2 D calls per recording, $N=49$ recordings), 298 O calls (6.1 ± 0.8 per recording, $N=49$ recordings), 394 M calls (8.0 ± 0.6 per recording, $N=49$ recordings), 1,524 H calls (31.1 ± 1.1 per recording, $N=49$), and 1,511 L calls (30.8 ± 1.1 per recording, $N=49$). Seal size (larger or smaller seals) was a random effect and the month of the recording (November or December) was a fixed effect. Likelihood ratio tests using the “anova” function were used to select the optimal model, and the bootstrap method was used for the inference tests for the fixed effect of month.

The inference tests showed that there was no evidence of the fixed effect, month, on the variability (SE) in the number of calls per vocalizing bout ($P=0.8$) or the number of D ($P=0.25$) and M calls ($P=0.45$). However, the inference tests showed that there was strong evidence for the effect of the number of vocalizing bouts in 30 min ($P=0.04$); the number of inter-calling periods ($P=0.02$); the mean number of calls within a vocalizing bout ($P=0.02$); the total number of calls ($P=0.03$); and the total number of O calls ($P=0.007$), H calls ($P=0.001$), and L calls ($P=0.001$).

When two models were applied (interaction effects) and both were significant, the best model was assessed based on the Akaike information criterion. Whether the data were normally distributed was determined by visually inspecting $Q-Q$ plots and scatterplots

of the residuals of the dependent variables; the O call data were log transformed to satisfy the assumption of normality. All tests were run in R, and factors were considered to have a statistically significant influence if $P < 0.05$. All means are given with their SEs.

Results

Number of vocalizing bouts produced within 30 min

The interaction model had the lowest AIC value (AIC = 212.2) and showed that there was an interaction between size and month (Table 2). The larger seals did not alter their number of vocalizing bouts between November and December, but the smaller males produced the same number of vocalizing bouts as the larger seals early in the breeding season, that is, in November. These seals increased the number of vocalizing bouts later in the breeding season, that is, December ($P = 0.01$; Figure 2A).

Number of inter-vocalizing (resting) periods

The interaction model had the highest support (AIC = 212.3; $P = 0.007$) and showed that there was an interaction between size and month on the number of inter-vocalizing periods, indicating break periods of more than 30 min. Both the smaller and larger seals took the same number of breaks over a 30-min period early in the breeding season, but the smaller seals increased the number of breaks, taking more breaks in December than in November.

The larger seals did not change the number of breaks during the breeding season (Figure 2B).

Mean number of calls per vocalizing bout

The interaction model had the strongest support, that is, the lowest AIC value (Table 2, 264.9), so there was strong evidence of an interaction effect ($P = 0.021$) of month and the size of the seal. The larger males produced bouts with the same mean number of calls throughout the season, whereas the smaller males produced bouts with a higher number of calls in November. However, the number of calls per bout dropped to below that of the larger seals later in the breeding season, that is, in December (Figure 2C). There was no evidence ($P = 0.06$) that the variability (SE) in the number of calls within a bout was influenced by either month or the size of the seal (Table 2), but there was evidence of an interaction effect ($P = 0.054$, Table 2) of the size of seal and the month on the rate at which the total number of calls were produced. The smaller seals produced more calls than the larger seals earlier in the breeding season, in November, but the number of calls dropped below that produced by the larger seals at the height of the breeding season, in December (Figure 2D).

Calling rate of the call types

There was no evidence of any interaction ($P = 0.35$, Table 2) between the size of the seal and the month on the rate at which the seals produced the D call. However, there was strong evidence of an interaction effect ($P = 0.003$, Table 2) between the size of seal and

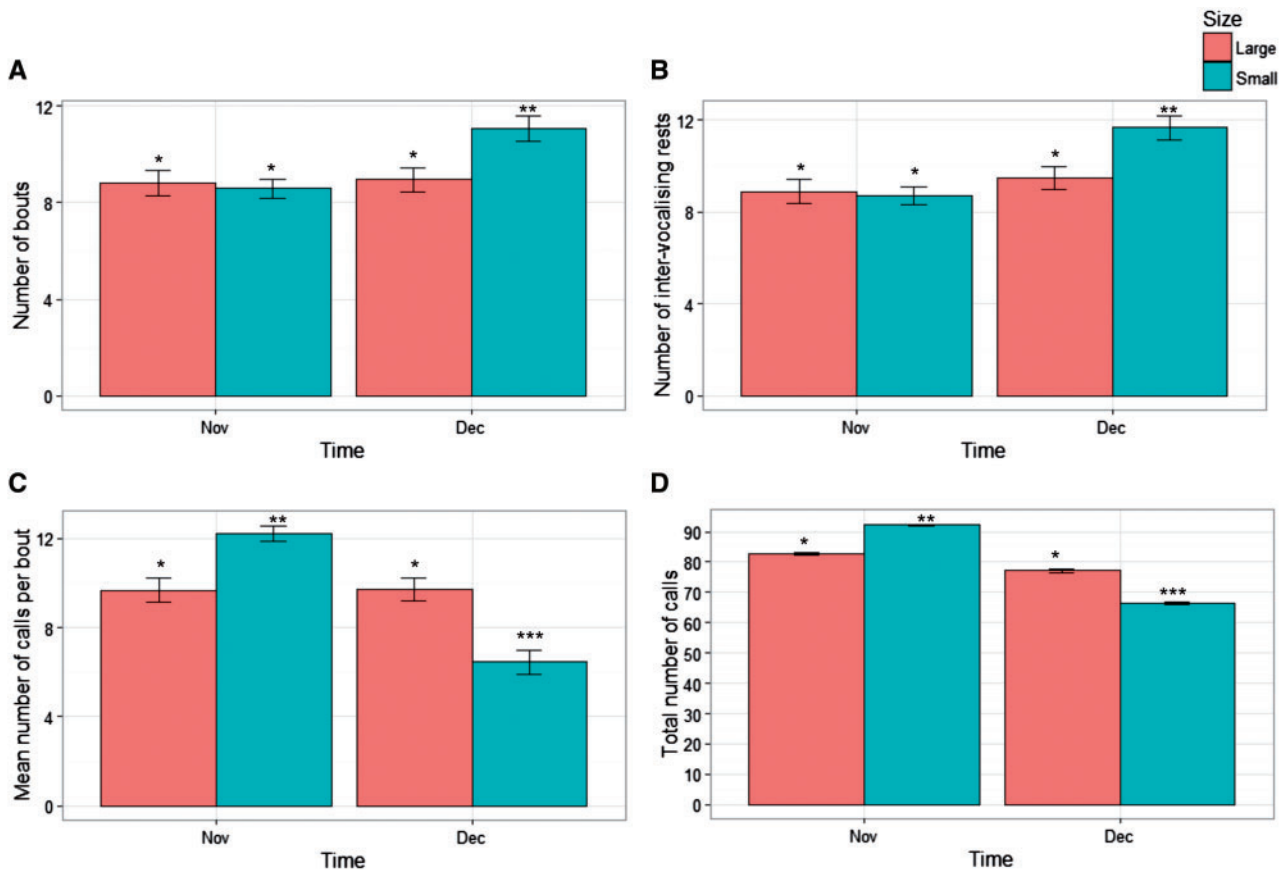


Figure 2. The influence of the seals' size (large; small) and the time within the breeding season (early = Nov; peak = Dec) on the male leopard seals' calling behavior (Mean \pm SE) over 30 min, including: (A) the number of vocalizing bouts, (B) the number of inter-vocalizing (resting) periods, (C) mean number of calls per vocalizing bout, and (D) the total number of calls produced. * indicates where significant differences ($P < 0.05$) occur between bars.

Table 2. Influence on calling patterns

Models	df	AIC	BIC	LogLik	Deviance	χ^2	df	P
Number of vocalizing bouts in 30 min								
Size + Month	4	217.2	224.8	-104.6	209.2	2.6	1	0.101
Size + Size*Month + Month	6	212.2	223.5	-100.1	200.2	9.0	2	0.011
Number of inter-calling breaks								
Size + Month	4	219.8	225.4	-105.1	210.2	3.53	1	0.060
Size + Size*Month + Month	6	212.3	223.7	-100.2	200.3	9.9	2	0.007
Mean number calls per bout								
Size + Month	4	268.7	276.2	-130.3	260.7	0.0	1	0.871
Size + Size*Month + Month	6	264.9	276.3	-126.5	253.9	7.8	2	0.021
Variability (SE) in the number of calls per bout								
Size + Month	4	82.3	89.9	-37.2	74.3	3.5	1	0.063
Size + Size*Month + Month	6	85.0	96.3	-36.5	73.9	1.3	2	0.515
Total number of calls in 30 min								
Size + Month	4	442.9	450.4	-217.4	434.9	0.2	1	0.662
Size + Size*Month + Month	6	441.2	452.6	-214.6	429.2	5.8	2	0.054
Number of D calls								
Size + Month	4	192.9	200.5	-92.5	184.9	1.2	1	0.284
Size + Size*Month + Month	6	194.8	206.2	-91.4	182.8	2.1	2	0.346
Number of LogO calls								
Size + Month	4	32.9	40.5	-12.5	24.9	0.1	1	0.900
Size + Size*Month + Month	6	24.9	36.3	-6.5	12.9	12.0	2	0.003
Number of M calls								
Size + Month	4	289.6	297.2	-140.8	281.6	1.8	1	0.186
Size + Size*Month + Month	6	293.4	304.7	-140.7	281.4	0.2	2	0.887
Number of H calls								
Size + Month	4	336.9	344.5	-164.4	328.9	0.1	1	0.907
Size + Size*Month + Month	6	329.8	341.1	-158.9	317.8	11.1	2	0.004
Number of L calls								
Size + Month	4	337.8	345.4	-164.9	329.8	0.7	1	0.395
Size + Size*Month + Month	6	331.5	342.9	-159.8	319.5	10.3	2	0.006

Notes: Comparison of the level of support for explanatory mixed-effect models used to examine how the leopard seals' size, the time within the breeding season, or the interaction between size and time, influenced the calling behavior of the male seals or the rate at which each call type is produced. AIC = Akaike information criterion; BIC = Bayesian information criterion; LogLik = log-likelihood.

the month on the rate at which the seals produced the O call (LogO). The smaller seals reduced the rate at which they produced the O call in December, that is, later in the breeding season, relative to November; the larger seals were more conservative and did not change the rate at which they produced the O call (Figure 3A). There was no evidence of an effect ($P=0.89$, Table 2) between the size of the seal and the month on the rate at which the seals produced the M call, but there was strong evidence of an interaction effect ($P=0.004$, Table 2) between the size of the seal and the month on the rate at which the seals produced the H call (Figure 3B). The smaller seals reduced the rate at which they produced the H call in December, that is, later in the breeding season, relative to November, while the larger seals did not (Figure 3B). There was strong evidence of an interaction effect ($P=0.006$, Table 2) of the size of the seal and the month on the rate at which the L calls were produced. The smaller seals produced more L calls than the larger seals earlier in breeding season, that is, in November, but the number of L calls dropped below that produced by the larger seals at the height of the breeding season in December (Figure 3C).

Discussion

Why call at a stable rate?

Larger male leopard seals produced calls at a stable rate throughout the breeding season, and they did not change their stereotyped calling pattern in terms of the number of vocalizing bouts, the inter-

vocalizing (rest) periods, or the rate at which they produced specific call types. This was in contrast to the smaller males, which exhibited less stable calling behavior. Earlier in the breeding season, in November, the smaller seals produced more calls than the larger seals, but by the height of the breeding season, in December, the smaller seals had reduced their call rates to below those of the larger seals. The production of vocalizations in long, consistent sequences is a trait that was sustained through the breeding season only by the larger seals, which suggests that it may be a costly signal.

In some species, higher call rates may be preferred by females when selecting a mate because males with higher call rates are easier to locate or the calls may reflect male status (McComb 1991). In male-male competition, higher call rates may be used during different stages of a conflict (McElligott and Hyden 1999) or as an honest advertisement by the winning opponent (Clutton-Brock and Albon 1979). Call rates may also be influenced by audience effects; an individual may alter its vocal behavior in response to surrounding individuals. For example, fallow bucks produce higher groaning rates when in the presence of females than in the presence of other males (McElligott and Hyden 1999). However, the consistent call rates of the larger male leopard seals throughout the breeding season may reflect an incentive not to expend excessive energy and avoid fatigue at the peak of the season. The timing of estrus in the females is asynchronous and extends over a three- to four-month period. The stability in the calling behavior of larger males suggests that they

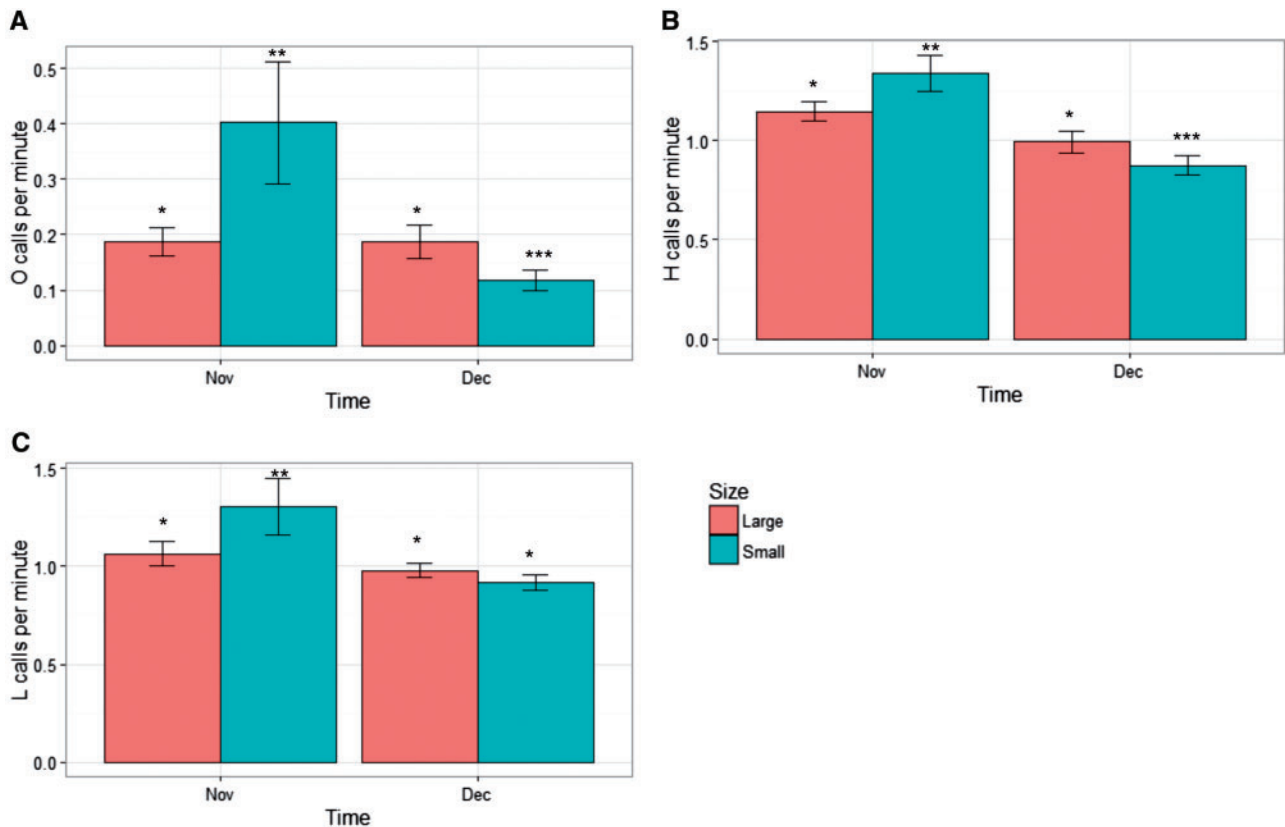


Figure 3. The influence of the seals' size (large; small) and the time within the breeding season (early = Nov; peak = Dec) on the rate (Mean \pm SE) at which male leopard seals produced the (A) O, (B) H, and (C) L calls per minute within a 30-min period. * indicates where significant differences ($P < 0.05$) occur between bars.

adopt a consistent calling rate strategy to prolong calling throughout the breeding season.

Stamina—Male leopard seals call underwater for hours each day over the breeding season. In aquatic-mating pinnipeds, the competition between males likely becomes more intense toward the height of the period during which females enter estrus (Rogers 2003; Van Parijs 2003). Although there is a higher likelihood of female leopard seals entering estrus in December, at the time that pups are weaned, females are likely to become sexually receptive at any time from late October through early January (Rogers 2009). Seasonal changes, including increases in vocal activity, associated with the onset of the breeding season have been observed in many mammals, including the hooded seal *Cystophora cristata* (Ballard and Kovacs 1995), the harbor seal (Van Parijs et al. 1999), the bearded seal (Van Parijs et al. 2001), the Australian fur seal *Arctocephalus pusillus* (Tripovich et al. 2008a, 2009a, 2009b), and the Weddell seal *Leptonychotes weddellii* (Collins et al. 2005; Rouget et al. 2007; Van Opzeeland et al. 2010).

Communicating over large distances—It may be advantageous for male leopard seals to maintain aquatic territories because it is difficult for them to predict the distribution of females in estrus. The pack ice floes on which the female seals haul out to give birth and raise their pups drift with the wind and current, and female leopard seals do not congregate in a single area but are widely dispersed throughout the Antarctic pack ice. For the signals from males to be received by sexually receptive females, the calls must propagate over extraordinarily long distances. Although the seals are distributed at low densities (Southwell et al. 2008; Forcada et al. 2012; Rogers et al. 2013), male calls are loud (Rogers 2014) and some at a

relatively low frequencies (i.e., 200 Hz; Rogers 2007), so they can propagate for long distances underwater.

Competing with noise—Under optimal sound propagation conditions, such as those of the Antarctic pack ice environment, multiple overlapping calls from many calling leopard seals have been recorded (Van Opzeeland et al. 2010; Rogers et al. 2013). The stable calling rates and repetitive vocal displays of male leopard seals may have evolved to counteract information loss due to transmission in noisy environments. Regularity increases the chance of detection (Terhune and Ronald 1986), and stereotyped acoustic displays are less affected by external influences within the marine environment. It has been suggested that these patterns serve as a means of reducing the masking effects of a noisy environment due to either environmental noise or the calls of conspecifics (Moors and Terhune 2004). The vocal characteristics (i.e., frequency-based information) of male leopard seal calls do not show clear individual variation (Rogers and Cato 2002); instead, the individually distinctive call sequences, which are less affected by signal degradation when communicating over long distances, may increase the probability of receiver recognition given these poor signal-to-noise ratios. The individually distinctive call sequences used by the male leopard seals likely drive the constant call rate.

Small seals exhibit a variable call rate

Smaller seals exhibited less stable calling behavior than the larger seals. Early in the breeding season, in November, the smaller seals produced long bouts with more calls, and at that time, their calling rates were substantially higher than those of the larger male seals.

However, by the height of the breeding season, the smaller males produced bouts with fewer calls and took more rests, that is, had longer inter-vocalizing periods, than the larger seals. The rates at which the smaller males produced calls dropped in December, which coincided with the peak in potential mating opportunities. The change included a lower mean number of calls in shorter vocalizing bouts, and the smaller males also reduced the number of the more commonly heard calls, the L and H calls, in December to produce the shorter vocalizing bouts.

The smaller male seals were presumed to be sexually mature because in pinnipeds, the calls by males that are associated with breeding emerge with the onset of sexual maturity; this has been observed in the walrus (Verboom and Kastelein 1995), the bearded seal (Davies et al. 2006), the Australian fur seal (Tripovich et al. 2008b, 2009b), and the Weddell seal (Collins et al. 2006) as well as the leopard seal (Rogers et al. 1996). The calls of young, sexually immature seals are used for mother–pup recognition (Collins et al. 2006) and are not part of the repertoire of sexually mature seals.

Advertising fitness

Bout length likely advertises the breath-holding capacity of the caller; the smaller seals were engaging in shorter bouts at the height of the breeding season, in December, while the larger seals were able to continue to produce the longer bouts that included more calls than produced by the smaller seals. At this time, the smaller seals produced more bouts over the same 30-min period; each bout consisted of fewer calls, and the smaller seals took more rest periods between bouts (inter-bouts). It is presumed that the smaller leopard seals are younger and presumably less socially dominant animals. In the bearded seal, young seals (i.e., captive seals) produce shorter bouts with fewer call types than wild seals (Davies et al. 2006).

Alternately, the smaller male seals' may change their vocal behavior as a result of the intensification of male agonistic encounters in December during the peak timing of the females' receptivity, because of higher competition among males. The smaller males are likely young animals and/or subordinate compared with the larger males. The larger, presumably dominant males might be more aggressive toward the smaller males. The change in vocal strategy of the smaller seals, to produce fewer calls and take more rests, might make them less localizable by the larger males, and thus avoid direct agonistic interactions and risks of injury.

The sites in the Antarctic pack ice that were identified as having lower leopard seal densities by concurrent visual and acoustic surveys were occupied by seals producing calls typical of larger seals. The lower densities may reflect the dominance of the larger individuals (Rogers et al. 2013), potentially indicating that they hold aquatic territories, although territorial behavior has not been confirmed in leopard seals. In the bearded seal, males commence vocal activity much earlier than their spring mating season, and this is believed to be due to the establishment of territories and dominance hierarchies by the males and/or seasonal changes in hormone levels (Davies et al. 2006; MacIntyre et al. 2013). For potentially the same reasons, that is, to establish underwater territories, male leopard seals commence vocal activity much earlier than the December mating season peak. Some leopard seals roam over large distances (Forcada and Robinson 2006; Kuhn et al. 2006; Gray et al. 2009), but typically both male and female leopard seals have been shown to exhibit a high degree of site fidelity (Rogers et al. 2005; Meade et al. 2015). Male leopard seals, similar to the bearded seal, may use their vocal behavior to maintain aquatic territories during the austral spring. Conversely, the areas in the Antarctic pack ice with

higher leopard seal densities were acoustically identified as being populated by smaller seals (Rogers et al. 2013), which have been observed to be more spatially tolerant and thus found at higher densities (Rogers and Bryden 1997).

Why higher pack ice calling is recorded in December

The conservative call rate of the larger seals and the reduction in call rates by smaller seals in December to levels lower than the larger seals suggest that the higher numbers of leopard seal calls recorded in December in the Weddell Sea (Van Opzeeland et al. 2010) are not likely due to a change in leopard seal calling rates. Although the number of calls detected in the Weddell Sea changed, the relative proportion of each call type remained constant (Van Opzeeland et al. 2010), which indicates that the calls were produced by leopard seals in other areas at constant rates. The December peak in leopard seal calls could be due to different drivers. First, it could be due to an intensification of agonistic encounters among males (Van Opzeeland et al. 2010); although the consistent calling rate suggests that the seals are not changing the rate at which they produce calls, males may be calling for longer periods. This would mean that there is greater chance for different seals to be calling at the same time. An alternate explanation for the higher December calling rate could be changing ice conditions as the pack ice and, by extension, the home range of the leopard seal, expands during the winter months (Rogers et al. 2005; Meade et al. 2015). Throughout the austral summer, the breeding season of the leopard seal, the pack ice contracts along with the size of the leopard seal home range (Rogers et al. 2005; Meade et al. 2015). In December, at the height of the breeding season, the ice is at a yearly minimum, so there is less habitat available to the seals. The higher December calling rate could reflect an increase in the density of leopard seals; in the bearded seal, higher call activity was correlated with higher sea ice concentrations (MacIntyre et al. 2013). Alternatively, an interaction between the intensification of male agonistic encounters and greater leopard seal densities may drive this change.

In conclusion, calling in a predictable, repetitive fashion may be advantageous for long-range communicators, particularly where the distribution of females during the breeding season is unpredictable in space and time. For marine mammals that call underwater, calling sequences advertise the breath-holding ability of the male, which may be related to stamina and endurance and thus advertise fitness. The breakdown in the calling stereotypy of smaller males at the height of the breeding season may represent an honest signal that could be widespread in other species.

Animal Ethics

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