Aquatic Mammals 2006, *32*(2), 175-181, DOI 10.1578/AM.32.2.2006.175

Stereotyped Calling Patterns of a Male Weddell Seal (*Leptonychotes weddellii*)

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Abstract

Underwater calling behaviour between breathing bouts of a single adult male Weddell seal (*Leptonychotes weddellii*) was examined with respect to call type and timing late in the breeding season at Davis Station, Antarctica. Underwater calls and breathing sounds were recorded on 1 and 8 December 1997. Thirty-seven sequences of calls prior to surfacing to breathe and 36 post-submerging sets of calls were analyzed with respect to probability of call type occurrence and timing. Dives were 461 ± 259 s (mean ± S.D.). The seal called every 29.7 ± 56.2 s throughout a dive. The first call after submerging was usually (n = 29 of 36) a low frequency (< 0.8 kHz) growl. Three patterns of three- to five-call type sequences were made following 28 of 36 breathing bouts. Call type patterns after submerging exhibited fewer different sequences than those before surfacing ($\chi^2 = 61.42$, DF = 4, $p < 0.000001$). The call usage patterns before surfacing were diverse and did not indicate when the seal was going to surface, a time when he would be vulnerable to attack from below. Our findings suggest the hypotheses that territorial male Weddell seals call throughout each dive and use stereotyped call patterns to identify themselves while vocally asserting dominance.

Key Words: Weddell seal, *Leptonychotes weddellii*, underwater vocalisations, songs, territorial defence, Davis, Antarctica

Introduction

Breeding territories are typically established by conflict resolution and then maintained and defended using long-range signals. These signals will function well if they achieve both species and individual recognition (Bradbury & Vehrencamp, 1998). Throughout the winter and breeding season, dominant male Weddell seals (*Leptonychotes weddellii*) defend breathing holes and underwater territories vocally with a variety of calls, including the male-specific loud, long, descending frequency "trill" (Kooyman, 1981; Thomas & Kuechle, 1982; Thomas et al., 1983; Bartsh et al., 1992; Oetelaar et al., 2003; Rouget, 2004). Territorial male Weddell seals sometimes share breathing holes (Kooyman, 1981), but similar to harbour (*Phoca vitulina*), spotted (*P. largha*), and bearded (*Erignathus barbatus*) seals, dominant male Weddell seals typically defend single underwater territories; vocalise regularly; and perform short, shallow display dives during the breeding season (Van Parijs, 2003). One way of combining both species and individual recognition in territorial defence calls would be to arrange shared call types into distinct stereotyped patterns (Bradbury & Vehrencamp, 1998).

Weddell seals congregate at breathing holes in 2-m thick landfast ice. This often requires a seal to displace another in order to breathe. In addition to biting hind flippers, the changeover between seals at a breathing hole may be facilitated by vocal signals prior to arriving at the hole (Evans et al., 2004; Rouget, 2004). This raises the possible advantage of a surfacing call being given before a breathing bout.

Some Weddell seals lying on the ice will close their mouths and nostrils and produce underwater call types. Although the behavioural function of such calling is unknown, it has enabled linking specific call types to the sex of the caller (Oetelaar et al., 2003). Recordings of the underwater call types made by individual Weddell seals on the ice occurred in clusters of one to six call types, but there were no stereotyped call sequences (Terhune et al., 1994).

Previous reports have indicated that Weddell seals occasionally produce sequences of underwater calls that are termed songs (Green & Burton, 1988; Morrice et al., 1994). There were an unknown number of seals in the water when Green & Burton (1988) and Morrice et al. (1994) obtained their underwater recordings of Weddell seals. Call sequences made by an individual seal may have been obscured by the intervening calls of others.

For the study reported here, the underwater call patterns of a single Weddell seal were recorded for a few hours on two different dates late in the breeding season. A two-channel system used a hydrophone to record the underwater calls and an in-air microphone enabled a determination of when the seal was breathing at the surface. The findings present new information with respect to the presence and stereotyped nature of songs within male Weddell seal repertoires and suggest that dominant males may call continuously throughout their dives.

Materials and Methods

In early December 1997, we conducted an opportunistic study of the transmission of underwater calls through sea ice. The goal was to determine if seals on the ice could hear the underwater calls (Terhune, 2004). Simultaneous recordings were made underwater and above the ice near a breathing hole. A male seal (identified by his use of trills; Oetelaar et al., 2003) frequented the breathing hole during the 2 d that recordings were obtained. In addition to recording sound levels of the underwater calls just above the ice, the in-air microphone recorded the breathing sounds when the seal surfaced in the hole. During analysis, it became apparent that a number of call types were given in regular short sequences, especially after the seal submerged following a breathing bout. It also seemed likely that all of the recordings were from a single adult male Weddell seal. We analyzed the recordings with respect to the timing and types of calls relative to the breathing bouts.

Recordings were made on landfast sea ice (68° 34.2' S, 77° 55.6' E), 1.55 km from the shoreline of Davis Station, Eastern Antarctica, on 1 and 8 December 1997. The water depth was 23 m. The ice in this area had been broken up and refrozen following the arrival of the *R.S.V. Aurora Australis* to the station two months earlier. There were at least five adult Weddell seals (two of each sex and one whose sex was unknown) in the area in November. No pups were born in the area. Recordings were made on an opportunistic basis at two different breathing holes (one per day). On 8 December, two adult female Weddell seals were hauled out 4 and 20 m, respectively, from the recording site, and an adult seal of unknown sex was hauled out 50 m away. One 2-h recording was made between 2010 h and 2210 h on 1 December, and 5.5 h of recordings were made between 0945 h and 1550 h on 8 December. A 2-h recording made on 9 December did not detect any high amplitude calls and was dropped from the analysis. There was no precipitation during the recordings, and winds were variable.

Simultaneous recordings in air (using a Radio Shack 33-2050 sound level meter as a microphone) and under water (Brüel and Kjær 8100 hydrophone with a Brüel and Kjær 2635 charge preamplifier) were made using a Sony TCD-D7 DAT recorder. The microphone was 1.0 to 3.0 m from the breathing hole, and the hydrophone was deployed through the breathing hole to a depth of 3.0 to 3.8 m. To reduce possible human disturbance, 2-h DAT tapes were used, and after the equipment was operating, the observer left the area.

The spectrograms of in-air and underwater sounds were examined using *Gram*, *Version 6.0.8* (R. S. Horne, 2001). The start and end time and number of breaths of each breathing bout were measured using the in-air breathing sounds as an identifying guide. The start time and call type of all clearly recorded underwater vocalisations were noted. The calls were classified into nine broad call types (Thomas & Kuechle, 1982; Pahl et al., 1997; Figure 1). Within one broad type, type L (growls), the seal only produced three mutually exclusive call subtypes, which were termed low roars (LR; frequency < 0.8 kHz), medium roars (MR; frequency 0.8 to 1.5 kHz), and high roars (HR; frequency > 1.5 kHz) (Figure 1).

Standard descriptive statistics were used to determine the mean and standard deviations associated with time between breathing bouts and number of breaths per bout. Pearson product moment correlations were used to examine the relationship between dive duration and the number of breaths. The time of each of the last five calls while ascending before a breathing bout was compared with the first five calls upon descent after a breathing bout. One set of five calls, which included an outlier value of 11.6 min between the second and third calls before surfacing, was removed from this analysis. The times of calls immediately before and after a breathing bout were compared to a random sample of between call times using ANOVA.

The probabilities of certain call types occurring immediately before or after a breathing bout and occurring in a particular sequence were examined by calculating Z scores using the probability of the occurrence of each call type in the total data set. The numbers of different sequences of one to five call types before and after the breathing bouts were examined using χ^2 analysis.

Results

On 1 and 8 December, a Weddell seal regularly surfaced to breath at the hole where the recordings were being made. Recordings were obtained prior to 38 surfacings and after 36 submergences. The time between breathing bouts averaged 7.7 ± 4.3 min (range 4.7-25.2 min, $n = 33$). There were two longer times (97 and 91 min, respectively),

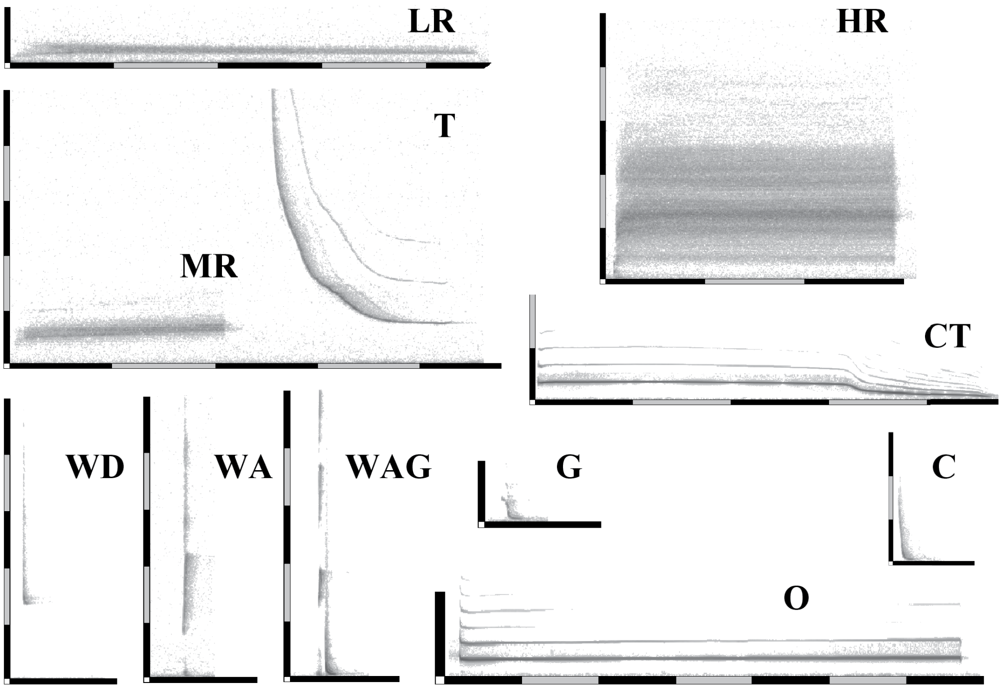

Figure 1. Sound spectrograms of Weddell seal call types: LR = low frequency roar, MR = middle frequency roar, HR = high frequency roar, T = trill, CT = trill with a constant frequency start, WD = whistle descending frequency, WA = whistle ascending frequency, WAG = whistle ascending grunt, G = guttural glug or grunt, C = chug, and O = tone (Thomas & Kuechle 1982; Pahl et al., 1997; see text); vertical dark bars = 2 kHz, horizontal dark bars = 2 s, and analysing bandwidth = 21.5 Hz.

each at the start of the last two recordings on 8 December, when there were no breathing bouts. In the first of these, the first call occurred 57 min into the recording; and in the second, the seal surfaced to breathe without any underwater calls being detected. There was a positive correlation between the dive duration and the number of breaths (15.0 ± 2.9 breaths per breathing bout, range = 11 to 36) following each dive ($r = 0.61$, $t = 4.34$, $p = 0.00014$, $n = 33$).

There were no instances of two seals using the breathing hole at the same time, and the shortest dive time was 4.7 min. The breathing bout prior to the longest time between calls (1,006 s) was not recorded (start of the second tape on 8 December). The second longest time between calls (696 s) occurred when the time between breathing bouts was 1,510 s. The seal may have been hauled out at another hole at this time.

There was a clear distinction between the received levels of the calls. Calls of a presumably distant seal were faint and were not analyzed. The calls occurring before or after a breathing bout all had higher received levels and were distinct. None of the higher amplitude calls were overlapped by another high amplitude call. No underwater calls were made when the seal was breathing at the surface. Throughout the 1 and 8 December recordings, all but one of the breathing bouts were preceded, and all were followed, by high amplitude calls. Exhalations and inhalations were distinguishable, and both had abrupt beginnings and endings. Occasionally, the seal made a small splash when submerging.

The mean time between the start of consecutive calls was 29.7 ± 56.3 s (range 1 to 1,006 s, n = 649). There were 37 recordings immediately prior to surfacing and 36 recordings after submerging. The number of calls between diving and surfacing ranged from 11 to 26. The times of the last call before surfacing, the first call after submerging, and the first call following a randomly selected call were similar ($F_{(2,103)} = 2.67$, $p = 0.07$; Table 1).

Of the 653 calls recorded on 1 and 8 December, the number of each call type ranged from 97 for chugs (C), 86 for LR, and 85 for descending whistles (WD) to low counts of 27 for grunts (G) and 20 for high roars (HR). Of the 36 instances of calls that followed a breathing bout, LR occurred first 29 times (Table 2). Using the total call count to determine the probability of a particular call type occurring, the probability of a random call being an LR is 0.132. The probability of 29 of 36 calls being LR is extremely low (Z = 11.939, $p < 0.000001$). Similarly, the probability of the first two calls after submerging being an LR followed by an HR (14 instances of 36) is also extremely low (Z = 36.16, $p < 0.000001$). Most of the call sequences following a breathing bout are clearly nonrandom (Table 2).

Nine of the 37 calls given just before surfacing were WAGs (Table 2). The probability of this being due to chance is low (Z = 1.8105, $p = 0.035$). This is less so for the last call being CT five times (Z = 1.657, $p = 0.048$) or WD five times (Z = 0.928, $p = 0.177$).

The most common long call sequence following submerging was LR - HR - MR - T - WAG;

Table 1. Timing (s, mean ± SD) of underwater calls by a Weddell seal before and after a breathing bout and following a random selection of calls (*n* = 36 in all cases)

Order of call	Before surfacing	After submerging	Random
First	22.7 ± 7.7	15.6 ± 9.3	20.6 ± 19.4
Second	38.8 ± 19.4	33.2 ± 9.6	56.3 ± 31.0
Third	55.9 ± 25.1	69.5 ± 24.4	73.3 ± 34.0
Fourth	73.3 ± 29.1	87.7 ± 28.8	105.8 ± 37.4
Fifth	98.0 ± 34.5	114.2 ± 36.5	129.4 ± 36.6

Table 2. The underwater call sequences, arranged in order of similarity, of a male Weddell seal immediately before (*n* = 37) and after (*n* = 36) a breathing bout; the numbers indicate the occurrences of each sequence; see Figure 1 for call names.

n	Fifth Last				Last	Breathing	First				Fifth	*n*
2	WAG	LR	WA	O	CT	*	LR	HR	MR	T	WAG	9
1	WA	O	LR	O	CT	*	LR	HR	MR	T	C	2
1	O	LR	WD	O	CT	*	LR	HR	MR	T	LR	1
1	WAG	T	G	WD	CT	*	LR	HR	WAG	LR	WA	1
1	WAG	CT	G	G	G	*	LR	HR	O	MR	T	1
1	C	O	O	O	WAG	*	LR	WA	WD	C	C	7
1	WD	CT	CT	O	WAG	*	LR	WA	WA	WD	C	1
1	T	WD	WD	O	WAG	*	LR	C	C	WD	CT	2
1	CT	MR	WD	O	WAG	*	LR	C	C	MR	T	1
1	O	G	CT	G	WAG	*	LR	C	C	O	T	1
1	C	C	WD	CT	WAG	*	LR	C	C	LR	WD	1
1	C	O	LR	WD	WAG	*	LR	C	T	C	C	1
1	G	G	G	T	WAG	*	LR	T	WAG	LR	T	1
1	G	O	LR	T	WAG	*	MR	C	MR	T	WA	1
1	WD	WD	O	CT	WA	*	MR	C	T	LR	C	1
1	WAG	O	LR	T	WA	*	WAG	LR	WA	WD	C	1
1	WD	CT	O	LR	WD	*	WAG	LR	WD	C	C	1
1	WD	C	O	LR	WD	*	C	LR	WA	WD	C	1
1	C	C	O	LR	WD	*	C	WD	WD	WA	CT	1
1	LR	T	T	WD	WD	*	C	WD	WD	WA	CT	1
1	T	O	CT	MR	WD	*						
1	CT	MR	WD	O	C	*						
1	T	MR	WD	O	C	*						
1	CT	MR	WD	LR	C	*						
1	LR	WA	WD	C	C	*						
1	CT	MR	WD	C	C	*						
1	WD	O	C	T	C	*						
1	LR	WD	CT	WAG	T	*						
1	WD	O	C	WAG	T	*						
1	O	G	O	LR	T	*						
1	O	CT	MR	WD	T	*						
1	MR	WD	O	C	T	*						
1	WA	WD	C	C	T	*						
1	LR	HR	O	MR	T	*						
1	WD	O	G	LR	HR	*						
1	O	C	O	T	HR	*						

Table 3. Number of call type sequence combinations by a Weddell seal that occurred immediately before or immediately after surfacing to breathe; the number of possible combinations is limited by the number of samples such that the first and last call can be one of the 11 call types, and the number of possible combinations of the first or last pair, etc., will be the sample size (i.e., only 37 or 36 of the possible 112 pairs of the 11 call types).

Before surfacing		After submerging	
Last call	8 of 11 possible	First call	5 of 11 possible
Last pair	24 of 37 possible	First pair	9 of 36 possible
Last three	30 of 37 possible	First three	15 of 36 possible
Last four	34 of 37 possible	First four	19 of 36 possible
Last five	36 of 37 possible	First five	20 of 36 possible

it occurred after 9 of the 36 breathing bouts. Two other times the WAG was replaced by a C. The sequence LR - HR - MR - T was recorded on all four tapes on 1 and 8 December. The second most common five-call sequence was LR - WA - WD - C - C, which occurred seven times. The numbers of the most common call sequences before and after a breathing bout are shown in Table 2. There were 12 sequences of LR - HR - MR - T, seven sequences of LR - WA - WD - C, and five sequences of LR - C - C following a breathing bout (Table 2). For the two most common call types, LR and C, the probability of these occurring in this order is 0.019. This pair occurred six times in the 36 post-dive call sets—well above the chance level of 0.68 occurrences.

The number of call types and different two- to five-call sequences given immediately before and after the breathing bouts are shown in Table 3. There were only two instances of a five-call sequence (WAG - LR - WA - O - CT) prior to surfacing (Table 2). There were many fewer call sequences after the breathing bouts than before ($\chi^2 = 61.42$, DF = 4, $p < 0.000001$; Tables 2 & 3).

Discussion

It was not possible to positively identify the Weddell seal in the water or to determine if there was more than one Weddell seal making the high amplitude underwater calls. Evidence which supports there only being one male seal making these calls includes (1) the regular use of trills, which denote the caller was a male (Thomas & Kuechle, 1982; Oetelaar et al., 2003); (2) three seals were hauled out on 8 December and, with the occasional faint trill from a distant male overlapping the loud calls reported herein, all of the seals observed here earlier in the season were accounted for; (3) the absence of underwater calls during breathing bouts; (4) there were no overlapped, high amplitude calls; (5) the shortest dive time was 4.8 min; and (6) the average dive time of 7.7 min was similar to mean dive durations (8.26 and 7.01 min, respectively) reported from two adult male Weddell seals fitted with depth-modulated acoustic transmitters (Harcourt et al., 2000). The two long periods of times without any calls on the afternoon of 8 December may have been associated with the male Weddell seal hauling out at a different breathing hole or swimming out of range. Because male Weddell seals are often aggressive (Bartsh et al., 1992), it is likely that only a single male was using the breathing hole at the recording site. For purposes of this discussion, it is assumed that all of the calls that were recorded during this study were made by a single, adult male Weddell seal.

When the seal was using the breathing hole at the recording site, he dove repeatedly and called regularly throughout each dive. The long quiet periods at the beginning of the second and third recordings on 8 December were not associated with dives at the recording location. Those periods and one other during which there was a silence of 1,006 s (16.7 min) aside, the seal called approximately every 30 s throughout the dives (Table 1). During the breeding season, territorial harbour and bearded seal males also call regularly while performing short dive displays, and they occupy areas that exhibit little overlap with those of other males (Van Parijs et al., 1997, 2003; Van Parijs, 2003). The maintenance of aquatic display areas via performing regular vocal and diving displays likely have male-male competition and female attraction functions (Van Parijs, 2003).

The most common calling behaviour produced by the Weddell seal in this study was an LR immediately upon descent. The call sequences after diving exhibited three common patterns with some variation, especially in the fourth and fifth call type (Table 2). Overall, only five call types were presented first after submerging. Beyond that, there were many fewer two- to five-call patterns of calls than would be expected by chance (Table 3). There was only one five-call sequence that occurred twice before the seal surfaced. The call sequences upon descent were more stereotyped than those that preceded surfacing. In the case of a male Weddell seal defending a territory, it could be a disadvantage to advertise when he was going to breathe. While breathing in a hole in the sea ice, the seal would leave his hind flippers and genital area undefended. Weddell seals occasionally bite each other throughout the winter

(Rouget, 2004), and male-male attacks during the breeding season often result in injury to one of the combatants (Bartsh et al., 1992).

The behavioural function of call sequences may be to allow individual identification of the caller and, thus, to enhance the breeding potential and related territorial defence functions of the calls. Many of the call types in the sequences used by the male Weddell seal at Davis are associated with territorial defence functions (Thomas et al., 1983). The WAG call type is only common at Davis (Abgrall et al., 2003), and its behavioural function has not been identified. The males of many avian and mammalian species that defend mating territories have individually specific calls (Bradbury & Vehrencamp, 1998). Stirling et al. (1987) present evidence that male Atlantic walruses (*Odobenus rosmarus*) produce individually specific vocalisation sequences, including distinctive diving calls. Among phocids, male bearded seals exhibit individuality in their trills (Van Parijs et al., 2003).

Green & Burton (1988) identified sequences of calls, which they termed songs, in their 1984 recordings, but not from another set of recordings made a year earlier. Morrice et al. (1994) report a greater number of songs, which exhibited diversity and variation in the call sequences. In these recordings, there were an unknown number of vocalising seals. These reports of Weddell seal songs indicate that the call type patterns differ. The call sequences reported in Green & Burton (1988) and Morrice et al. (1994) also differ from those reported here. This study indicates that individual male seals produce more than one sequence of call types.

Individually instrumented male and female Weddell seals were recorded at McMurdo Sound (Evans et al., 2004). A female seal produced C and "chirps" (a type of WD in the classification terminology used in this study; Thomas & Keuchle, 1982) later in the dive when close to the ice under the surface, when examining novel objects, or when approaching a breathing hole. A male seal only vocalised (T, G, C, WD, and clicks) during ascent in the last half of a dive (Evans et al., 2004). A marked difference between the two sets of observations is that the seals recorded by Evans et al. made only a few calls, and these occurred only in the last half of a dive; while in our study, the male produced stereotyped vocalisations upon descent at the start of the dive and others throughout the dive. One possible explanation for the differences in calling patterns of the respective male seals may be that in our study, the male had 2 mo to establish his dominance at the breathing hole, while the male at McMurdo Sound had been relocated in association with the study.

Male Weddell seals establish and defend breathing holes from freeze-up in early winter to the end of the breeding season. These holes are shared with females, juveniles, and—presumably in the winter—submissive males. Seals sometimes waited under a hole that was occupied by another seal and occasionally nipped the hind flippers of the seal at the surface (Rouget, 2004). Some underwater call types used by females and submissive males may facilitate changeover at the breathing hole (Evans et al., 2004; Rouget, 2004).

The findings reported herein raise the possibility that dominant male Weddell seals produce a series of diving calls, presumably in association with the defence of their territory. This would be similar to the behaviours of territorial bearded and harbour seals that vocalize regularly during short display dives throughout the breeding season (Van Parijs et al., 1997, 2003).

We speculate that the individual male Weddell seal recorded at McMurdo Sound (Evans et al., 2004) may have been a submissive, transitional, or non-territorial male (Bartsh et al., 1992) that was not calling regularly in an attempt to establish a territory. The observations from the Davis seal provide support for the hypotheses that dominant male Weddell seals vocalise regularly throughout their dives, exhibit stereotyped songs at the start of the dives, and do not indicate when they are about to surface. Larger sample sizes will be required before these hypotheses can be appropriately tested, however.

Acknowledgments

The Australian Antarctic Division provided full logistical support at Davis. The field work was assisted by the 1997 expeditioners at Davis, especially T. Cheesman. The Natural Sciences and Engineering Research Council of Canada provided financial support for this research via a Discovery grant to JT. AD travelled to Canada with the assistance of the Biodaqua student exchange program. V. Hayes, S. Van Parijs, J. Thomas, K. Dudzinski, and an anonymous reviewer for this journal are thanked for helpful comments on an earlier draft of this manuscript.

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