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Underwater Call Sequences of Weddell Seals (*Leptonychotes weddellii*) at the Vestfold Hills, Antarctica

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Abstract

Repeated sequences of different call types have been reported in some recordings of underwater calls of Weddell seals (*Leptonychotes weddellii*) but not others. Recordings made during the breeding seasons of 1990 (1 site, n = 1,136 calls), 1991 and 1992 at three and seven sites, respectively (n < 210 calls per study site) at the Vestfold Hills, Antarctica, were examined. Calls were classified into 16 types, and series of calls were examined for two data sets (1990) and for all years. The low number of seals at these breeding sites resulted in a long series of calls with no overlap, thus facilitating the opportunity for sequence analyses. At most, but not all, study sites there was a three-call-sequence that occurred above chance levels. Thirty-five of 43 three-call-sequences were only detected in one year at one recording location; the other eight were heard at up to four study sites in the same year. Five sets of three-call-sequences occurred in the reverse order of other sequences. Pairs of calls were common, and most occurred in one order and not the reverse. During 3 h of observations of a male-female pair of Weddell seals lying quietly in a pool, there were no sequences of calls or dueting (n = 241 calls). Our findings support the hypothesis that some Weddell seals make nonrandom series of calls, but the functional significance of these patterns is uncertain. Because similar sequences occurred at several study sites, however, it is not likely that call sequences could be used as a natural acoustic tag to identify individual seals.

Key Words: underwater vocalizations, call sequence, song, breeding behaviour, Vestfold Hills, Antarctica, Weddell seal, *Leptonychotes weddellii*

Introduction

Weddell seals (*Leptonychotes weddellii*) breed on land-fast ice surrounding Antarctica. During the breeding season (October to December), dominant males establish underwater territories (Stirling, 1969; Kaufman et al., 1975; Thomas et al., 1983; Bartsh et al., 1992) in areas where breeding females haul out. Male and female Weddell seals call throughout the breeding season. They have a large and geographically variable underwater call repertoire (Thomas & Kuechle, 1982; Pahl et al., 1997; Abgrall et al., 2003). The functional significance of most call types is unknown, but trills are thought to be associated with male territorial defense (Thomas & Kuechle, 1982; Thomas et al., 1983).

Short sequences of call types were first reported by Thomas & Stirling (1983). Songs (sequences of calls) were detected by Green & Burton (1988) in their recordings from one year, but not another. Morrice et al. (1994) reported sequences of calls after the end of the breeding season. On the ice, individual Weddell seals commonly made groups of in-air closed mouth calls (typical of the underwater repertoire; for social interactions on the ice, seals produce open mouth calls) and two- and three-call-sequence sounds, but the order of the call types was variable (Terhune et al., 1994). A single, male Weddell seal made a stereotypical series of calls with predictable timing between calls at the beginning of dives (Terhune & Dell'Apa, 2006). Other studies have shown stereotypical patterns in various species of marine mammals (i.e., leopard seals [*Hydrurga leptonyx*], Rogers & Cato, 2002; bearded seals [*Erignathus barbatus*], Ray et al., 1969; Atlantic walruses [*Odobenus rosmarus rosmarus*], Stirling et al., 1987; killer whales [*Orcinus orca*], Miller et al., 2004; and humpback whales [*Megaptera novaeangliae*], Payne et al., 1983). Terrestrial mammals also produce stereotypical call sequences (e.g., Taï chimpanzees [*Pan troglodytes*], Crockford & Boesch, 2005). Stereotyped sequences of call types may serve to identify individuals in the absence of individually specific features of a single call type. Male bearded seals produce trills that exhibit clear individual variation (Van Parijs et al., 2003). Within-call variation has not been reported for Weddell seals, in part because of difficulties in assigning specific calls to individual males.

Terhune & Dell'Apa (2006) reported that the sequencing of calls by a single male Weddell seal occurred immediately after a breathing bout and that call types made later in the dive had no pattern. If such sequencing forms an integral aspect of a dominance display, they should be produced often, regardless of dive behavior. At breeding sites where there are a large number of seals in the water, it would be difficult to identify sequences from individuals because of call overlap from other seals. Most Weddell seal breeding sites in the Vestfold Hills, Eastern Antarctica, are small groups and have low numbers of seals in the water (McFarlane, 1996). As a result, most calls are not overlapped, which facilitates identification of call sequences. While it is not usually possible to determine which individual seal is vocalizing, stereotyped series of call types should be detectable (Green & Burton, 1988; Morrice et al., 1994).

If male Weddell seals are using a sequence in their territorial display, this would enable a male to produce a unique pattern that would serve to identify him individually. There were at least three different sequences made by a single male just after diving, but not all such calls were arranged into patterns (Terhune & Dell'Apa, 2006).

The purpose of this study was to examine the underwater vocalizations of Weddell seals for evidence of stereotypical short sequences and to determine if such sequences were shared among individuals.

Materials and Methods

Recording and Analysis Procedures

Underwater calls of Weddell seals were recorded in the Vestfold Hills (68° 20' to 68° 35' S and 77° 55' to 78° 25' E) during the 1990, 1991, and 1992 breeding seasons (Figure 1). A single breeding group at Study Site 0 (Figure 1) was recorded in 1990 (Terhune et al., 2001), and three and seven breeding groups were recorded at Study Sites 1, 3, and 5 in 1991 and at Study Sites 1 through 7 in 1992, respectively (Pahl et al., 1997). The 1990 recordings were made using a "tombstone sonobuoy" hydrophone, a Sony WMC3 cassette recorder, and Sony UX100 or TDK SA90 cassette tapes (system frequency response was from < 0.10 to > 10.00 kHz, but the linearity of the system was unknown). Recordings from 1991 and 1992 were made using a Sony Walkman WM-D6C cassette recorder (frequency response was linear from 0.04 to 15.00 kHz ± 3 dB) and an ITC 6050C hydrophone (built-in preamplifier, frequency response was linear from 0.03 to 75.00 kHz ± 1 dB), or a Brüel & Kjær 8100 standard measuring hydrophone with a Brüel & Kjær 2635 pre-amplifier (frequency response was linear from 0.02 to 32.00 kHz ± 1 dB). Cassettes used were TDK SA90, Sony HF-ES90, or Sony UX100. Recordings were made opportunistically at various times throughout the day and evening when there was low wind and no precipitation. For analysis, all recordings were played back using a Sony stereo cassette player (model TC-K510) and Sony MDR-CD480 headphones. A real-time spectral analysis was simultaneously viewed using the program *Gram* (R.S. Horne, Version 6.0.8) and a standard computer.

For each underwater call, the type, start time (sec), and presence/absence of call overlap were recorded. Time was measured from the display on the cassette player (accuracy to the nearest second). The calls were classified into 16 call types, some of which were more variable than others. Sound spectrograms of 11 of the most common types are presented in Terhune & Dell'Apa (2006). Common English phonetic names for these call types were descending frequency whistle (WD), trill (T), tone (O), chug (C), low-frequency roar (LR), ascending frequency whistle (WA), guttural glug or grunt (G), mid-frequency roar (MR), ascending whistle – grunt pairs (WAG), trill with a constant frequency beginning (TC), squeak (S), mew (M), high-frequency roar (HR), growl (L), knock (K), and whoop (Q). These call types were recorded and characterized previously by Thomas & Kuechle (1982), Pahl et al. (1997), and Oetelaar et al. (2003).

With the exception of the 1990 study site, two tapes from each study site were randomly selected from a larger set of recordings. The recordings selected were made between 28 November and 13 December 1991 and between 10 November and 10 December 1992. A total of 105 sequences were analyzed from each recording for a total of 210 calls per study site. Analysis start times were randomly selected between 2 and 12 min from the beginning of the tape. In cases where a tape did not contain 105 calls, the next tape recorded that day was analyzed from the beginning until the 105 calls were collected. The 1990 recordings were all from a single breeding group. Six recordings, each from a different day between 11 and 29 November 1990, were randomly selected for analysis. All of the calls detected in the full length of each of the six recordings were classified, resulting in a total of 1,182 calls of which 1,136 were not overlapped by other calls.

Three-Call-Sequences

Although a five-call-sequence was previously identified from a single male Weddell seal, three-call-sequences were more common (Terhune & Dell'Apa, 2006). Familiar three-call-sequences would be easier to identify if more than one seal

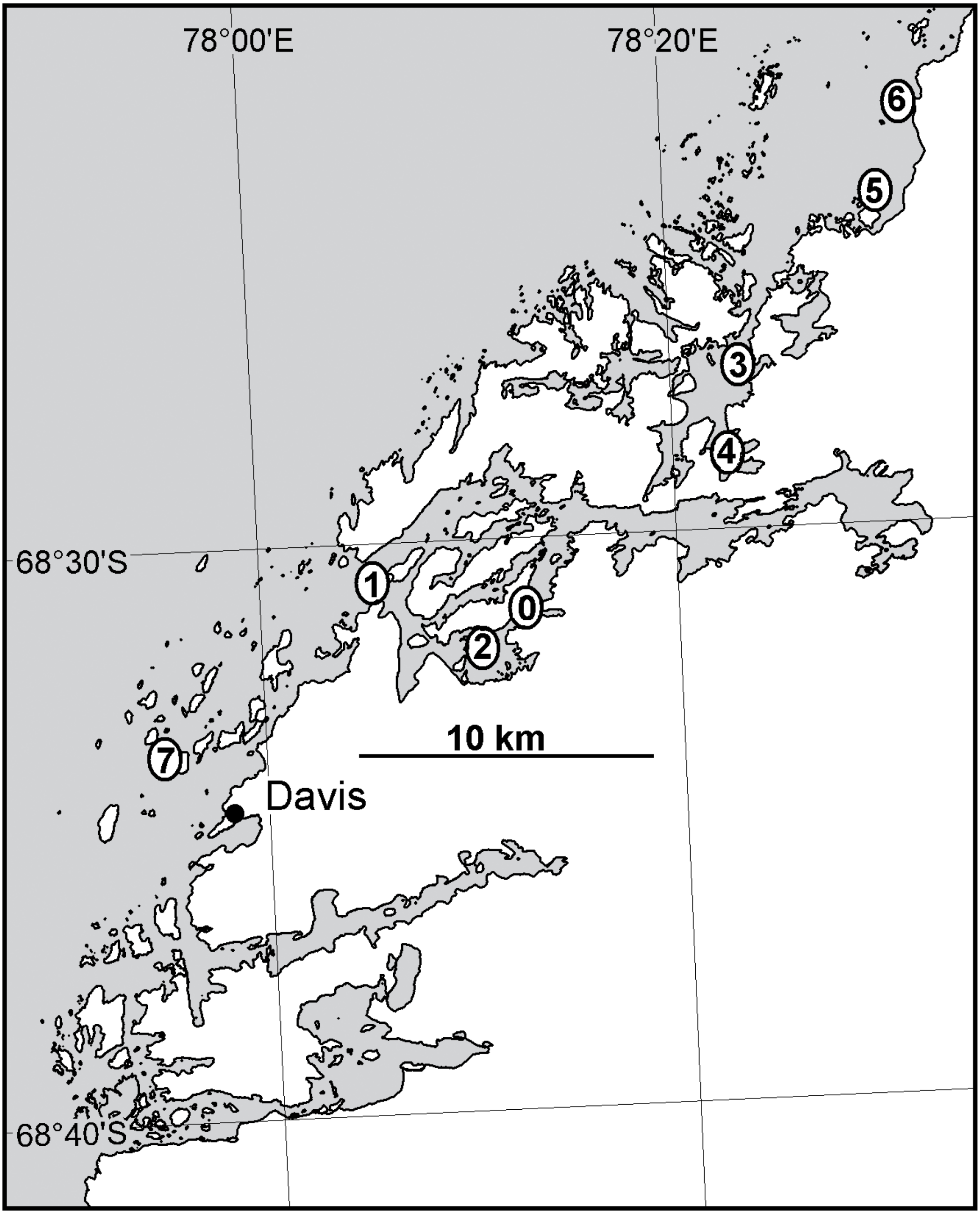

Figure 1. Weddell seal underwater recording locations in the Vestfold Hills (based on Australian Antarctic Division Map Number 13142)

was calling. Strings of calls that were not overlapped by other calls were identified. In cases where calls were overlapped, both were discarded from the data set. At least three non-overlapped calls had to occur between sets of overlapping calls to remain in the data set. That is, if two overlapping calls were followed by two non-overlapped calls and then followed by another two overlapping calls, all six were removed.

Because four- and five-call-sequences were possible, calls of the same type which occurred more than three times in a row were not counted more than once to avoid overcounting. In a few cases where there were long strings of similar call types, the time between calls was examined to determine if there were any natural breaks in the call production. In such cases, the calls would be assumed to make up two sets of three calls. For example, the call type sequences depicted in Figure 2 would be grouped into the following sequences: CT-T-T, T-T-T, then after a quiet period of 3 min, T-T-T, T-T-O, T-O-O, O-O-WD, and O-WD-CT. The first WD and the WA and G calls would not be counted because they overlapped, and only one set of T-T-T before the 3-min quiet period would be counted (Figure 2).

Data sorting (*Statistica 6.1*, StatSoft Inc., Tulsa, Oklahoma, USA) was used to identify repeated three-call-sequences. For each recording, a list of the call types in the sequence in which they occurred was prepared. The list was copied twice, with each subsequent list being staggered by one call. Thus, each call and the two calls that followed it were arranged in order. Because overlapped calls had been removed and calls at the end of one recording were not joined with the first call of the next recording, there were gaps in the sets of three calls. These gaps were removed prior to sorting. A standard sorting technique (*Statistica 6.1*) arranged the most similar sequences, and these were counted. For the majority of the calls (i.e., those that occurred in long, uninterrupted sequences), each call would appear as the first, second, and third call in a series of 3 three-call-sequences. This double counting was adopted because there was no way of determining when a three-call-sequence would begin.

The probability of three calls in a series occurring together more often than expected by chance was calculated. The number of each call type was divided by the total number of calls to give a probability of occurrence of that call (Table 1). The probabilities of the three specific call types in a song were then multiplied to give the probability of these three calls occurring in a group. Using these probability values and the sample sizes for each recording location, the numbers of three-call-sequences likely to occur by chance were calculated for each common three-call-sequence (Table 2). Only sequences that occurred at least five times at the 1990 study site or at least three times at the other recording locations were considered because fewer sequences per study site could be attributable to chance. Within this data set, the presence of mirror image (reversed) groupings of call types was noted. A chi-square goodness-of-fit test was used to compare the numbers of each three-call-sequence per study site with the numbers expected by chance. The 1990 sample

Table 1. Number and probability of occurrence of the Weddell seal underwater call types from 1990, 1991, and 1992 data sets

Call type	Number analyzed	Probability of occurrence
WD	630	0.206
T	413	0.135
O	408	0.133
C	317	0.103
LR	292	0.095
WA	291	0.095
G	216	0.071
MR	97	0.031
WAG	92	0.030
TC	89	0.029
S	56	0.018
M	47	0.015
HR	40	0.013
L	39	0.013
K	32	0.010
Q	4	0.001
Total	3,063	

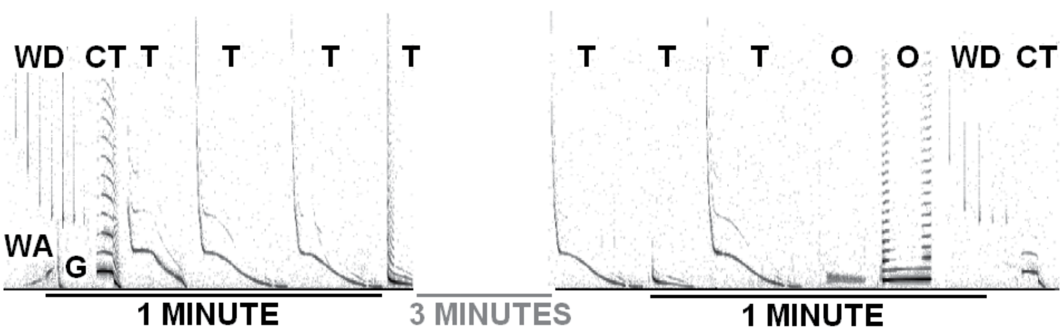

Figure 2. Sound spectrograms of Weddell seal underwater call type sequences; the selection of individual calls and the time between adjacent calls has been significantly reduced for diagrammatic purposes. See text for explanation of call type labels and the manner in which three-call-sequences were identified.

Table 2. Most common sequences of three consecutive underwater Weddell seal calls recorded at breeding sites (see Figure 1) in the Vestfold Hills, Eastern Antarctica in 1990, 1991, and 1992; the numerator = observed count, denominator = expected, assuming a random distribution of calls. Underlined values are above chance levels; 1990, $n = 1{,}136$ calls, other sites, $n < 210$ calls, chi-square test: df = 1, Bonferroni correction $p < 0.001$. **Bolded** three-call-sequences also occur in the reverse order.

Sequences			Location										
Call types			Site-Year										
First	Second	Third	0-90	1-91	3-91	5-91	1-92	2-92	3-92	4-92	5-92	6-92	7-92
O	O	O	27/2.7	--	--	--	--	--	--	--	--	--	--
O	MR	T	13/0.6	--	--	--	--	--	--	--	--	--	--
O	WA	WD	11/3.0	--	--	--	--	--	--	--	--	--	--
WD	**O**	**O**	10/4.1	--	--	--	--	--	--	--	--	--	--
O	WD	O	9/4.1	--	--	--	--	--	--	--	--	--	--
O	**O**	**WA**	9/1.9	--	--	--	--	--	--	--	--	--	--
O	WA	WA	8/1.4	--	--	--	--	--	--	--	--	--	--
WA	WD	WD	8/4.6	--	--	--	--	--	--	--	--	--	--
WD	T	WD	--	--	--	--	--	--	7/1.2	--	--	--	--
T	T	T	--	--	--	--	--	--	7/0.5	--	--	--	--
T	O	O	7/2.7	--	--	--	--	--	--	--	--	--	--
WA	O	WA	7/1.4	--	--	--	--	--	--	--	--	--	--
TC	TC	TC	7/0.03	--	--	--	--	--	--	--	--	--	--
WD	O	MR	6/1.0	--	--	--	--	--	--	--	--	--	--
O	**O**	**WD**	6/4.1	--	--	--	--	--	--	--	--	--	--
O	WA	O	6/1.9	--	--	--	--	--	--	--	--	--	--
WA	**O**	**O**	6/1.9	--	--	--	--	--	--	--	--	--	--
WD	**T**	**T**	--	--	--	--	--	--	5/0.8	--	--	--	--
T	**WD**	**WD**	--	--	--	--	--	--	5/1.2	--	--	--	--
T	**T**	**WD**	--	--	--	--	--	--	5/0.8	--	--	--	--
LR	MR	WD	5/0.7	--	--	--	--	--	--	--	--	--	--
WA	WD	O	5/3.0	--	--	--	--	--	--	--	--	--	--
WAG	O	LR	5/0.4	--	--	--	--	--	--	--	--	--	--
WD	T	LR	--	--	--	--	--	--	--	--	4/0.6	--	--
WD	**WD**	**C**	--	--	--	--	--	--	3/0.9	--	--	--	--
WD	C	WD	--	--	3/0.9	--	--	--	--	--	--	--	--
WD	LR	LR	--	--	3/0.4	--	--	--	--	--	--	--	--
WD	G	WD	--	--	3/0.6	--	--	--	--	--	--	--	--
T	O	T	--	--	--	--	3/0.5	--	--	--	--	--	--
O	WD	T	--	--	--	--	--	--	3/0.8	--	--	--	--
C	C	O	--	--	--	--	3/0.3	--	--	--	--	--	--
LR	WA	C	--	--	--	--	--	3/0.2	--	--	--	--	--
G	WD	G	--	--	3/0.2	--	--	--	--	--	--	--	--
G	S	G	--	--	--	--	3/0.02	--	--	--	--	--	--
WD	G	G	--	--	--	--	--	3/0.2	--	--	--	--	--
C	C	WD	5/2.5	--	--	--	--	--	--	5/0.5	--	--	--
WD	**WD**	**T**	--	--	--	--	--	--	6/1.2	3/1.2	--	--	--
T	WD	T	--	--	--	--	--	--	5/0.8	--	4/0.8	--	--
WD	C	C	5/2.5	--	--	5/0.5	--	--	--	6/0.5	--	--	--
C	**WD**	**WD**	--	--	--	--	--	--	--	4/0.9	--	3/0.9	--
C	C	C	--	--	--	3/0.3	3/0.3	--	4/0.3	--	--	--	--
C	WD	LR	--	--	--	3/0.4	--	--	--	--	3/0.4	--	--
WD	WD	WD	--	--	--	--	--	--	8/1.8	--	6/1.8	5/1.8	4/1.8

size was 1,136 calls, and the sample sizes of the other study sites were set at 210 calls when calculating the expected values. This latter number is conservative because some of the study sites had as few as 180 calls after the overlapping calls were removed. Because the chi-square test was performed 58 times, a Bonferroni correction was applied, and the level of statistical significance was set at $p < 0.001$.

To determine if individual males were recorded in more than one year, tag sighting data from 1990, 1991, and 1992 were obtained (H. R. Burton, Australian Antarctic Division, pers. comm.). Only four adult males were found in more than one year. Other males were present, but they moved around during the breeding season or were only sighted at one breeding site. Common call sequences and male tag numbers were compared to determine if any male was present at the same sites in the same years as these particular call sequences occurred.

Two-Call-Sequences

The order of pairs of call types was examined using the 1990 data set. Overlapping calls were removed and calls at the end of one recording were not joined with the first call of the next recording. The pairs of calls were determined by producing a list of the call types in order, then copying it staggered by one call. Data were sorted by pairs using *Statistica 6.1* to facilitate counting. For the majority of the calls (i.e., those that occurred in long, uninterrupted sequences), each call would appear as the first and then second call in a series. This double counting was adopted because there was no way of determining the beginning order of a pair.

The number of each pair, and when present, the same two call types in reverse order, were counted. Where there was a difference between the occurrences of a pair and the reverse order of the pair, a chi-square goodness-of-fit test was used to determine statistical significance. In this case, the expected value was assumed to be the mean of the two (Table 3). Because the chi-square test was performed 16 times, a Bonferroni correction was applied, and the level of statistical significance was set at $p < 0.003$.

Male/Female Pair

On 15 November 1997, an unusual occurrence of a large meltpool or pond of water overlying downward buckled sea ice was found at Study Site 1. There were two seals in this pool, and their underwater sounds could be clearly heard in air. The meltpool was 30 m long and 15 m wide. The ice sheet was bent downward from the seaward side, and the pool was deep enough that the seals could readily swim under the landfast sea ice at the surface on the landward side of the pool. The seals were observed on 15 November 1997 from 13:40 to 16:53 h sun time. In-air recordings were made for 170 min, with a 23-min break midway through the session. The observer was sitting or standing on the ice on the seaward side of the pool, midway between the seals. The underwater calls were clearly audible, and the observer indicated on the recording which seal had vocalized. The different coloured hind flipper tags of the two seals were observed while they were in the water, and the male seal had unique scar patterns.

Table 3. Numbers of pairs of Weddell seal underwater calls that reflect higher use of one order of call types over the reverse; the most common occurrences of pairs of calls and the occurrence of that pair in reverse order are noted. **Bolded** pairs occurred more often than chance (chi-square test: df = 1, Bonferroni correction $p < 0.003$).

Pair Call types	Number analyzed	Number reverse-order pairs	Number random pairs	Chi-square expected	(p)
O-MR	17	0	3.4	54.4	(< 0.0001)
MR-T	18	2	3.5	60.1	(< 0.0001)
WD-O	32	17	22.8	3.7	(0.06)
WA-WD	25	11	16.3	4.6	(< 0.03)
O-WA	27	18	10.5	25.9	(< 0.001)
L-TC	9	1	0.3	252	(< 0.001)
G-HR	8	1	0.8	64.8	(< 0.001)
TC-WD	6	1	5.0	0.2	(0.65)
TC-WAG	5	0	0.7	26.4	(< 0.001)
WD-G	11	6	12.2	0.1	(0.75)
MR-WD	8	3	5.3	1.4	(0.24)
LR-C	6	1	8.1	0.5	(0.48)
LR-MR	6	1	2.5	4.9	(< 0.03)
MR-WD	8	3	5.3	1.4	(0.24)
O-C	13	8	11.4	0.2	(0.65)
T-O	13	8	14.9	0.2	(0.65)

The seals were a male and likely a female. The female was not positively identified when in the water, but both had different coloured flipper tags and their sex had been determined when they were observed on the ice in the immediate vicinity earlier the same day. They were recorded using a hand-held Sennheiser ME66 microphone (frequency response was linear from 0.05 to 20.00 kHz ± 2.5 dB) fitted with an MZW 20 windscreen and a Sony DAT TCD-D7 tape recorder (frequency response was linear from 0.02 to 22.00 kHz ± 1.0 dB). A Sony PCM-R300 DAT recorder was used when analyzing these recordings.

Results

Observations at 1990-1992 Study Sites

The 1990 breeding site had 27 mother/pup pairs plus a few adult females without pups. There was one dominant male (without wounds) and a submissive male (often bleeding from open wounds) that remained at the site and at least nine other males that were present for short periods between 10 November and 6 December 1990. The 1991 and 1992 recording locations were visited less often by researchers; hence, the numbers of males present at each site are unknown.

Three-Call-Sequences

The 3,063 calls from all study sites were classified into 16 types. Four call types comprised 58% of the vocalizations while seven call types made up 10% of the recorded sounds (Table 1). There were 43 different three-call-sequences that occurred five or more times in the 1990 or three or more times in the 1991 and 1992 recordings (Table 2). Thirty-five of these three-call-sequences were only at one recording location, but 12 of these occurred near-chance levels. Eight three-call-sequences occurred at more than one recording location. These sequences were detected 20 times, but seven of the occurrences could be attributed to chance (Table 2).

Data from Study Site 0-90 contained 10 three-call-sequences at above-chance levels. None of these were commonly found at the other recording locations, but these study sites all had smaller sample sizes (Table 2). Study Site 3-92 had 5 three-call-sequences at above-chance levels that were not common elsewhere and 4 three-call-sequences that also occurred, sometimes at chance levels, at one to four other study sites. In contrast, no three-call-sequences occurred at above-chance levels at Study Sites 1-91, 6-92, or 7-92 (Table 2).

There were five sets of reverse-order sequences within the 43 three-call-sequences (Table 2). The sequences WD-T-T or T-T-WD and T-WD-WD or WD-WD-T all occurred at above-chance levels at one study site or more but were composed of the two most common call types, WD and T. Three-call-sequences (O-O-WA and C-WD-WD) occurred at above-chance levels at one study site or more, but their reverse-order sequences (WA-O-O and WD-WD-C) were not recorded. Finally, WD-O-O and O-O-WD only occurred at chance levels (Table 2). Otherwise, of the 43 different three-call-sequences, 31 occurred at above-chance levels. There were four examples where all three calls were made up of a single call type (O, T, C, and WD; Table 2).

The three-call-sequences possibly produced by the four tagged males were compared (Male 395 at Study Sites 0-90 and 2-92; Male 703 at Study Sites 1-91 and 7-92; Male 735 at Study Sites 5-91 and 2-92; Male 3428 at Study Sites 0-90, 1-91, and 2-92). There were no common three-call-sequences shared between any of these pairs of recording sites (Table 2). The males may not necessarily have been at the respective recording sites when the recordings were made, and Study Site 1-91 had no common call sequences.

Two-Call-Sequences

The order of call types was determined for 832 pairs. Within the 832 pairs identified, there were 139 different pairs of call types. Of these, nine were the same call type repeated twice, 82 were different call types, and an additional 48 pairs were the reverse-order pairs. Thirty-four pairs did not occur in the reverse order. Of these 34 pairs, 29 only occurred once or twice during recordings. The pairs which exhibited the greatest difference between the order of the call types are shown in Table 3. The two most common pairs of calls were O-MR and MR-T (Table 3). The sequence O-MR-T was the most common three-call-sequence at Study Site 0-90 (Table 2).

Male/Female in Meltpool

The male and female in the meltpool provided a unique recording opportunity. The seals were stationary or moving slowly back and forth along the length of the pool. The distance between them ranged from 2 to 30 m. The seals were often close enough to make it likely that they could see each other. They did not change ends of the pool. Both seals lay horizontally in the water, and aside from surfacing to breathe, they did not make any quick movements or come into physical contact.

A total of 241 calls were made by both seals at a rate of 1.4 calls/min. The female produced six different call types, mostly WD and G, while the male produced 10 different call types, mostly C and T (Table 4). On 15 occasions, the female produced a series of WD sounds just after the male began a C, T, TC, or O sequence. Because

Table 4. Number of calls made by a male and a female Weddell seal in close proximity to each other in a meltpool during the breeding season; recording time was 170 min. The calls were made under water, but recorded in air, while the two seals were lying quietly in a large pool of water (see text for details and call type definitions).

	Number of vocalizations by	
Call type	Male	Female
WD	7	24
T	44	0
O	8	0
C	69	5
LR	7	0
WA	0	2
G	15	25
MR	4	0
WAG	1	0
TC	19	0
L	5	1
Q	0	6
Total	179	62

most calls were well-spaced in time, no three-call-sequences were identified.

Discussion

Our findings on the presence of two- and three-call-sequences are consistent with previous observations of underwater vocal behavior in Weddell seals (Thomas & Stirling, 1983; Green & Burton, 1988; Morrice et al., 1994). Green & Burton (1988) observed that Weddell seals form vocalization sequences, but these sequences were not present in both years of their study. Our study also indicated that stereotypical three-call-sequences were not present in all years at each study site. The relatively few examples of the long sequences of stereotyped calls in many of the smaller data sets from 1991 and 1992 reflect the difficulty other authors had in identifying Weddell seal call sequences. Morrice et al. (1994) reported a greater number of songs, which exhibited diversity and variation in the call sequences. If individual males are making three-call-sequences with only a few call types, then it is more likely that songs will be identified as they were at Study Site 3-92.

An important difference between this study and others identifying patterns in marine mammal calls (e.g., Stirling et al., 1987; Rogers & Cato, 2002; Miller et al., 2004; Terhune & Dell'Apa, 2006) is the lack of knowledge of the identity, age, sex, and behaviours of the callers. Without knowledge of the start time of a calling behaviour, there is no reference point which can be used to predict the beginning of the sequence.

The occurrences of similar three-call-sequences at a number of study sites in a single year suggest that they are not made by an individual male. Some of the different three-call-sequences recorded at a single study site may have been made by a single seal, however. The diversity of three-call-sequences at two study sites, Study Site 0 in 1990 and Study Site 3 in 1992, suggest that individual male seals likely produce more than one sequence. This was the case for a single male seal recorded late in the breeding season near Davis Station (Terhune & Dell'Apa, 2006). In our study, it was impossible to determine if some two- or three-call-sequence patterns were from one or two seals as noted in some other marine mammals. Pairs of resident killer whales have shown a tendency to produce similar call types (Ford, 1989; Miller et al., 2004). Frequently, an individual called and a second individual repeated the same call type; however, the same individual often repeated a call twice (Miller et al., 2004). Miller et al. suggest dueting may function to help resident killer whales communicate position and movement trajectories to each other. They also suggest timing and type of call are influenced by the calls of others. For the pair of Weddell seals whose underwater calls were recorded in air, the female sometimes called in apparent response to the male's call, but there was no other evidence of dueting.

A study of male leopard seal calling patterns (Rogers & Cato, 2002) showed a tendency for the animal to make common call pairs with a specific order. The most common vocalization pair in our Weddell seal 1990 sample (O-MR) occurred more often than in the reversed order. Crockford & Boesch (2005) found a similar tendency for call pairs to occur in one order, but not the reverse, in Taï chimpanzees. Only a few call combinations occurred frequently, and Crockford & Boesch suggested that calls may be combined according to the situation. The tendency to produce call types in a particular order could lead to the formation of sequences containing three (or more) calls.

It is likely that trills are made only by males (Thomas & Kuechle, 1982; Thomas et al., 1983; Oetelaar et al., 2003). Since two- and three-call-sequences without trills were also found, it is possible that females and nonterritorial males also form stereotypical sequences. The function of sequences of underwater calls can only be assumed. Morrice et al. (1994) suggest that songs are used as dominance displays to indicate that an individual male is the holder of that territory. It is assumed that some call types, especially trills, made by dominant males have a territorial defense or sexual advertisement function (Ray et al., 1969; Kaufman et al., 1975; Thomas et al., 1983). Some other call types made by females and nonterritorial males likely have a submissive function (Thomas et al., 1983). The different call type usage by the male and female Weddell seal pair support assigning a submissive function to short whistles, a low intensity threat to grunts (the most common female calls), and territorial advertisement and/or an aggressive function to trills and chugs (the predominant male calls) as proposed by Thomas et al.

In a study of male leopard seals, Rogers & Cato (2002) attributed individuals to specific calling patterns. They suggested the function of individually distinctive patterns in leopard seals is to convey caller identity. Leopard seals are a more solitary species than Weddell seals, however; therefore, they have a greater need to communicate over long distances. Individually specific sequences of calls, rather than variation in acoustic characteristics, are less likely to be degraded over longer distances. Male Weddell seals may identify themselves by using stereotyped call sequences in conjunction with individual features within the calls. Such an analysis is beyond the scope of this study.

There were no three-call-sequences that could be attributed to any of the four males that were observed in more than one year. There were some study sites at which no common three-call-sequences were detected (in 180 to 200 calls). Other three-call-sequences were found at multiple study sites. Although one male Weddell seal produced a series of different three- to five-call-sequences (Terhune & Dell'Apa, 2006), another individually recorded male seal only produced a few calls in the latter half of a dive (Evans et al., 2004). This variation in individual vocalizing behaviour may be reflected in the presence and absence of the three-call-sequences recorded in 1991 and 1992. Also, it is not likely that call sequences could be used as a natural acoustic tag to identify individual seals.

Weddell seals produce a wide variety of underwater calls, with some types being more common than others. There appears to be a tendency to arrange pairs of calls in a particular order, but individual behaviours differ widely. Call-response duets between males and females may not occur. Studies using methods that permit attributing specific calls to individual seals of known sex and social status will be needed before the functional significance of the different call types and calling behaviours can be determined.

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