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ORIGINAL PAPER

Geographic variations in underwater male Weddell seal Trills suggest breeding area fidelity

John M. Terhune · Douglas Quin · Andrea Dell'Apa · Mandana Mirhaj · Joachim Plötz · Lars Kindermann · Horst Bornemann

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Abstract Adult Weddell seals (*Leptonychotes weddellii*) exhibit site fidelity to where they first breed but juveniles, and perhaps transient adult males, may disperse from their natal location. If there is mixing between adjacent breeding groups, we would expect that common vocalizations would exhibit clinal patterns. Underwater Trill vocalizations of male Weddell seals at Mawson, Davis, Casey, McMurdo Sound, Neumayer and Drescher Inlet separated by ca. 500 to >9,000 km, were examined for evidence of clinal variation. Trills are only emitted by males and have a known territorial defense function. Trills from Davis and Mawson, ca. 630 km apart, were distinct from each other and exhibited the greatest number of unique frequency contour patterns. The acoustic features (duration, waveform, frequency contour) of Trills from Neumayer and Drescher Inlet, ca. 500 km apart, were more distinct from each other than they were from the other four locations. General Discriminant Analysis and Classification Tree Analysis correctly classified 65.8 and 76.9% of the Trills to the correct location. The classification errors assigned more locations to sites >630 km away than to nearest neighbours. Weddell seal Trills exhibit geographic variation but there is no evidence of a clinal pattern. This suggests that males remain close to single breeding areas throughout their lifetime.

Keywords *Leptonychotes weddellii* · Weddell seal · Reproduction · Site fidelity · Underwater vocalizations · Geographic variation

Introduction

Weddell seal (*Leptonychotes weddellii*) females form small breeding groups close to breathing holes in the fast ice around Antarctica. Dominant males defend underwater territories below these holes (Kaufman et al. 1975; Siniff 1991; Harcourt et al. 2000). Submissive males are tolerated within or close by these territories by the dominant male, while transient males will move between breeding locations, presumably challenging territory holders (Bartsh et al. 1992). Observations from tagging studies indicate a pronounced breeding site fidelity to a preferred area for both male and female Weddell seals as they become older (Stirling 1974; Cameron et al. 2007). In contrast, juvenile Weddell seals of both sexes are thought to disperse away from their natal site (Croxall and Hiby 1983; Cameron and Siniff 2004). Weddell seals born

J. M. Terhune (✉)
Biology Department, University of New Brunswick,
P.O. Box 5050, Saint John, NB, Canada E2L 4L5
e-mail: terhune@unbsj.ca

D. Quin
dqmedia, P.O. Box 656, Browns Summit, NC 27214-0565, USA

A. Dell'Apa
Dipartimento di Scienze del Mare, Università Politecnica delle Marche, 60131 Ancona, Italy

M. Mirhaj · J. Plötz · L. Kindermann · H. Bornemann
Alfred Wegener Institute for Polar and Marine Research,
P.O. Box 12 01 61, 27515 Bremerhaven, Germany

Present Address:
A. Dell'Apa
CTS Ambiente-Settore Conservazione Natura, Via Albalonga 3,
00183 Rome, Italy

Present Address:
M. Mirhaj
Institute of Animal Production in the Tropics and Subtropics,
University of Hohenheim, Fruwirthstr. 12,
70599 Stuttgart, Germany

in Atka Bay near Neumayer Station have been observed on fast ice at Drescher Inlet, about 500 km away (J. Plötz, unpublished data). However, of a large number of pups that have been tagged near Davis Station, only a few tagged seals have been sighted about 130 km away in the Larsemann Hills (Pahl et al. 1997) while none have been sighted ca. 630 km away near Mawson Station (Abgrall et al. 2003). Nevertheless it seems likely that some transient males may venture farther along the coastline in search of females disposed to mate.

Weddell seal populations exhibit geographically related vocal repertoire and call usage differences around Antarctica (Thomas and Stirling 1983; Thomas et al. 1988; Terhune et al. 2001; Abgrall et al. 2003). However, direct comparisons of such variation between seals from distant breeding populations, over different years, are difficult as the numbers, sex ratios, reproductive states and related behaviours of the seals being recorded can vary (Esterby et al. 2000). Missing knowledge on behaviours and sample sizes is a problem for studies of geographic differences in marine mammal vocalizations.

Another technical difficulty in these comparisons is associated with measuring acoustic features of calls with very different structures (Terhune et al. 2001). If call types contain different features, it will not be possible to make direct comparisons between them as some measurements will not be possible on all call types within the data set. Weddell seal vocalizations exhibit a great deal of variation between and within call types (Thomas and Kuechle 1982; Pahl et al. 1997), with many multiple element calls exhibiting changes in frequency (kHz) and duration within individual call types (Thomas and Kuechle 1982; Moors and Terhune 2004). The durations of Weddell seal calls increase when the call is overlapped by another seal call (Terhune et al. 1994; van Polanen Petel et al. 2006). Thus call duration measures at low calling rates would be expected to be lower than those at high calling rates, independent of any geographical variation.

One way to reduce extraneous influences on geographic variation studies would be to select a single call type produced by only one of the sexes. This would enable researchers to obtain identical sets of acoustic measurements from all geographic locations and each call would likely have been emitted during similar behavioural contexts. Only male Weddell seals produce Trills (Thomas and Kuechle 1982; Oetelaar et al. 2003). The Trill function is related to territorial advertisement, breathing hole defence and may also serve to attract females (Thomas et al. 1983). Adult male Weddell seals at all geographic locations employ this call type. Trills belong to a broad classification category and exhibit variable features. However, all are long duration calls that have a significant drop in frequency (Thomas and Kuechle 1982).

Call patterns that are geographically distinct would likely occur if the breeding populations are isolated, while clinal variation in vocal traits along a coastline would be suggestive of regular contact among adjacent localities (Rossi-Santos and Podos 2006). If Weddell seal males are moving along the coastline then, via mixing, Trills from adjacent locations should be more similar to each other than to those from transcontinental populations. In this study, we examined Weddell seal Trills to determine if geographic variation in vocalizations among male seals is evident over distances of between 500 and more than 9,000 km of coastline.

Materials and methods

The study areas were near Mawson Station (67°S, 63°E), Davis Station (68°S, 78°E), Casey Station (66°S, 110°E), McMurdo Sound (78°S, 166°E), the PALAOA (Boebel et al. 2006) recording site near Neumayer Station (70°S, 8°W) and the Drescher Inlet (72°S, 19°W; Fig. 1). The distances along the coastline between pairs of adjacent locations, moving from Mawson eastward toward Drescher Inlet, were approximately 600, 1,600, 3,300, >9,000 and 500 km, respectively. Underwater recordings were collected in different years however they were all obtained during the Weddell seal breeding season. Recordings were collected in multiple years at Mawson and Davis and, within all but one year, samples were obtained from 3–7 different breeding groups per location (Table 1). The

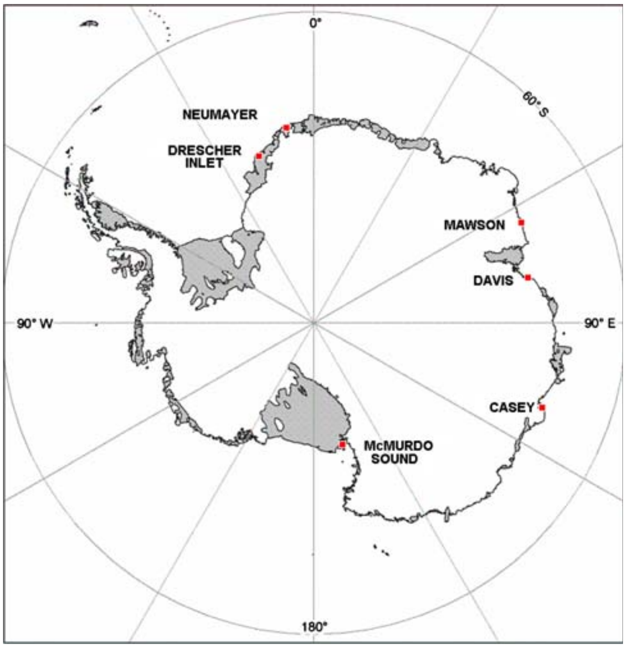


Fig. 1 Locations of the recording areas. Map based on map 13177, Australian Antarctic Data Centre

Table 1 Weddell seal underwater Trill recording locations and sample sizes

Location	Year	Number of breeding groups	Number of Trills analyzed
Mawson	2000	5	43
	2002	7	121
Davis	1990	1	17
	1991	3	60
	1992	6	120
	1997	7	69
Casey	1997	4	42
McMurdo Sound	1996	2	162
Neumayer	2006	Unknown	91
Drescher Inlet	2003	1	112

recordings from McMurdo Sound, Neumayer and Drescher Inlet were obtained in single years. Different sets of recording equipment were used and the frequency ranges of all systems were from below 60 Hz to 20 or 22 kHz.

Underwater recordings were randomly sampled for Trills in the following manner. A random number generator was used to select 10–20 (for small breeding groups) or 100–200 (for large breeding groups) time stamps per tape recording. The first Trill emitted after each random time stamp was re-recorded as a wav file at a sampling rate of 44 or 48 kHz. The numbers of Trills analyzed from individual breeding groups at Mawson, Davis and Casey were low (typically 10–20) because there were <30 adult females with pups and likely only a few males present. The small sizes of the breeding groups meant there was a high probability of obtaining multiple recordings from a single dominant male. The numbers of seals at the breeding sites in McMurdo Sound were higher allowing for more extensive sampling (Table 1).

Trills were defined as being single element calls (but see below) that were longer than 2 s and with a frequency drop of at least 1 octave (halving of the frequency) within the call. Trill structures were variable (Thomas and Kuechle 1982) and could contain sinusoidal (narrow bandwidth) or frequency modulated or pulsed (broadband) waveforms (Fig. 2). Trills were analyzed using the spectral analysis program Gram (R.S. Horne; version 6.0.8) with frequency and time resolutions of ±23 Hz and ±5 ms. Total duration was measured first. The frequency was then measured at the start and end of the Trill and at nine equally spaced intervals along the Trill (Fig. 2a). In the case of broadband signals, the frequency was recorded at the point of greatest amplitude where this was clearly evident, or the mid-point of the frequency band (Fig. 2b). Similarly for narrow bandwidth signals, the frequency was measured at the point of highest amplitude. For some of the longer Trills, there was a break in sound production near the middle or toward the end of the Trill. These breaks were <2 s. In a few cases, one of the eleven frequency measurement locations occurred during the break (Fig. 2a). These "broken" Trills were considered to be one call because the timing and frequency when the second part began was highly stereotyped and, at the respective bases, the recommencement of the Trill occurred at a predictable time and frequency. In those cases, the frequency assigned was at the appropriate time along a line between the end of the first section and the start of the second section. The coefficient of frequency modulation of each Trill was calculated using the formula:

CoFM = [(sum(from $t = 1$ to $t = n-1$) abs(ft−ft + 1)/$n-1$)/mean F]*100 (Harrington 1989) where t = number of each of the 11 frequency measurement locations, ft = frequency at that measurement point and mean F = mean of all frequency measurements. The waveform at the start and end of the Trill was classified as (1) sinusoidal, (2) frequency modulated or (3) pulsed (Fig. 2c; Thomas

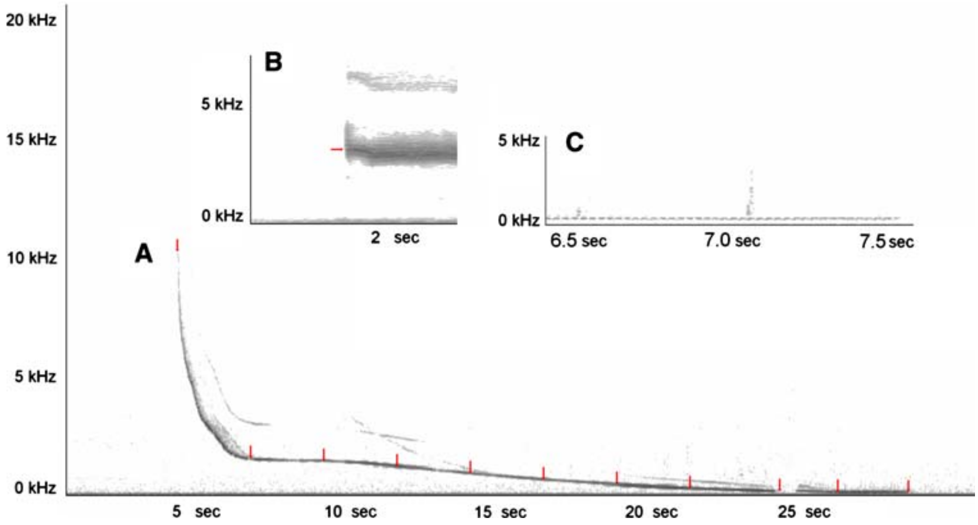


Fig. 2 Sound spectrograms of Weddell seal underwater Trills. **a** Trill with a sinusiodal waveform and the *vertical arrows* indicate the locations where the frequency measurements were made. Note that the *third arrow from the rights* falls at a "break" in the Trill. **b** A Trill with a frequency modulated waveform: the *arrow* shows where the frequency was measured. **c** A trill that ends with a pulsed waveform. Analyzing bandwidths were 43 Hz for **a** and **c** and 11 Hz for **b**

and Kuechle 1982; Pahl et al. 1997). Trills with poor signal to noise ratios which prohibited making repeated measurements within ±1 cursor step or which were masked by noise (ice noises or other seal calls) were not analyzed.

Statistical analyses

ANOVA or Kruskal–Wallis ANOVA was used to examine Trills recorded at the six locations for differences in: duration (s), start and end frequency, distribution of start and end waveform types (coded values), coefficient of frequency modulation (CoFM), frequency drop from start to finish of the Trill (All) and frequency drop between the first and second measurement positions of the Trill (First Pair). The duration and frequency measures were converted to log base 2 before the statistical tests were conducted. Log base 2 was selected because mammalian pitch discrimination typically operates on an octave-based system (see Terhune 1999). The log base 2 transformation for the duration measurements was used to reduce the variation within the measurements and convert the values to a scale which was similar in scope to that of the frequency measurements.

Pearson Product-Moment correlation was used to examine the relationship between CoFM and sample size per base. ANOVA and Kruskal–Wallis ANOVA were used to determine if the CoFM values differed between bases.

The drop in frequency for each Trill was calculated using the log base 2 frequency measures between the first and last (all) and first and second (first pair) frequency measures. ANOVA was used to test for differences in the frequency ranges per base.

The mean values of each of the above features were also ranked and analyzed using cluster analysis (Euclidean distance, unweighted pair-group average linkage) to determine which geographic areas had Trills that were most similar to each other. For continuous acoustic features, mean values were directly ranked in order from highest to lowest. Start and end waveforms per geographical location were ranked by assigning code numbers to the waveforms (sinusoidal = 1, frequency modulated = 2 and pulsed = 3). Average values were ranked from highest (indicating a larger proportion of pulsed and FM waveforms) to lowest (indicating a larger proportion of sinusoidal and FM waveforms).

The log base 2 frequencies (Hz) at the 11 positions per call were used in a series of *k*-means clusters to determine if the contour shapes of the Trills varied between locations. The clustering was set to sort at constant intervals. The number of clusters went from 2 to 30. The number of frequency contour shapes that were unique to one base were counted for each of the *k*-means clusters.

A General Discriminant Analysis (GDA) was performed on Trills from the six locations using two categorical factors (start and end waveform types) and 12 continuous predictors (duration and the 11 frequency measurements). Canonical scores were calculated for each Trill. Variations in the canonical scores in the different years at Mawson and Davis were also examined.

The Trills were also assigned to the different locations using Classification Trees (CT) based on univariate splits. The discriminant-based splits were performed using Statistica v 6.1, (StatSoft 2003). The stopping rule was that splitting continued until all terminal nodes were pure (all members from one recording location) or contained no more than 20 cases and then the branches were pruned using a backward stepwise elimination method. The $n = 20$ stopping rule was arbitrarily selected because it was larger than the call sample sizes at some individual recording locations and was less than half of the sample size from Casey. The procedure entails using random sub-samples for a cross-validation procedure. The analysis was performed 10 times, each with a different seed number for the random number generator and the classifications were averaged. Single analyses were also conducted using $n = 5$ and $n = 40$ stopping rules.

Results

A total of 837 Trills were analyzed and sample sizes per location were unequal (Table 1). Some of the longer Trills at Davis and Drescher Inlet exhibited a short break in sound production between the call's mid-point and near the end. When this happened with the Drescher Inlet Trills, the Trill began again a few Hz higher in frequency. Conversely, in the case of Davis Trills, the resuming frequency was a few Hz lower than before the break (Fig. 2a).

For all statistical tests, the assumption of independence of data probably was not met. It is extremely likely that more than one Trill was recorded from a single male and potentially a series of Trills from one male may have been recorded. Even though the Trills were selected randomly from the recordings made at each site, it is likely that a dominant male was present and calling throughout the recording session. Also, in the ANOVAs, the assumptions of homogeneity of variances were typically not met (after the duration and frequency measures had been transformed to log base 2). Thus, while the ANOVA results should be interpreted with caution, the ranks of the mean values in Table 2 will be valid.

ANOVA identified statistical differences in mean Trill duration ($F(5, 831) = 34.568$, $P < 0.0001$). Unequal N HSD post hoc testing revealed that the durations of calls at Drescher Inlet (Mean ± S.D.: 25.30 ± 14.54 s) were longer than Trills at the other locations ($P < 0.0001$; Mawson 11.00 ± 6.60, Davis 11.81 ± 10.29, Casey 15.01 ± 7.46, McMurdo Sound 11.57 ± 8.01, Neumayer 13.34 ± 2.08 s).

Table 2 Ranks of mean values of Trill features (1 = highest) between the six Antarctic locations

Location	Call feature							
	Duration	Start Freq.	End Freq.	CoFM	Start Wave	End Wave	Freq. Drop All	Freq. Drop First pair
Mawson	6	6	2	3	1	3	6	1
Davis	4	3	6	2	4	5	2	3
Casey	2	4	3	5	3	4	4	4
McMurdo Sound	5	2	4	4	2	2	3	6
Neumayer	3	5	1	6	6	6	5	5
Drescher Inlet	1	1	5	1	5	1	1	2

The mean start frequencies of the Trills differed ($F(5, 831) = 57.098$, $P < 0.0001$) from a low at Mawson (10.66 ± 1.15 octaves) to 12.00 ± 1.48 at Davis, 11.58 ± 1.17 at Casey, 12.38 ± 1.00 at McMurdo Sound, 11.42 ± 9.78 at Neumayer and 12.51 ± 1.02 at Drescher Inlet (note: 12.00 octaves = 4,096 Hz). The maximum analysis frequency at Drescher Inlet was 14.55 octaves while it was only 14.29 octaves at the other sites. These results could have been confounded somewhat by the higher digitizing sampling rate used for the Drescher Inlet recordings so the 20 cases with start frequencies above 14.29 octaves were removed from the analysis. Unequal N HSD post hoc tests indicated a significant difference between Mawson and Davis ($P < 0.0001$) and Neumayer and Drescher Inlet ($P < 0.0001$).

Leopard seal (*Hydrurga leptonyx*) calls were prominent at McMurdo Sound, Neumayer and Drescher Inlet but none were heard on the other recordings. At Drescher Inlet in particular, many of the ends of Trills could not be measured because of masking by low frequency leopard seal calls. The sample sizes in Table 1 do not include these calls. ANOVA revealed a significant difference in end frequencies between locations ($F(5,831) = 18.231$, $P < 0.0001$). Unequal N HSD post hoc tests indicated that the values at Davis (7.97 ± 1.51 octaves) were significantly lower than those at Mawson (9.07 ± 1.57 octaves; $P < 0.0001$). There were no differences ($P < 0.065$) between the ending frequencies at Casey (8.75 ± 1.59), McMurdo Sound (8.64 ± 1.07), Neumayer (9.13 ± 0.71) and Drescher Inlet (8.58 ± 1.32). The higher values at Mawson were related to some frequency contour shapes that increased in frequency towards the end of the Trill.

All three waveforms were equally represented at the beginning of the Mawson Trills. Sinusoidal and FM waveforms were equally represented at Casey. Sine waves and then FM were the most common start waveforms at Davis, Neumayer and Drescher Inlet. Most Trills at McMurdo Sound began with FM. Overall, Kruskal–Wallis ANOVA indicated a significant difference in the starting waveforms between bases ($H(5, N = 837) = 200.4$, $P < 0.001$). Within the Trills, transitions between the three waveforms occurred gradually and at different times.

Pulses were the most common ending waveform at Mawson, McMurdo Sound and Drescher Inlet, followed by FM. At Davis, the most common endings were sinusoidal and then pulses while at Casey FM was the most common ending, followed by pulses. At Neumayer the most common endings were sinusoidal and then FM. Overall, Kruskal–Wallis ANOVA indicated a significant difference in the ending waveforms between bases ($H(5, N = 837) = 232.1$, $P < 0.001$).

There was a significant difference in the mean coefficients of frequency modulation (CoFM) between locations ($F(5, 830) = 29.047$, $P < 0.00001$). The CoFM was highest at Drescher Inlet (4.82 ± 2.15) followed by Davis (4.26 ± 1.77), Mawson (3.79 ± 1.38), McMurdo Sound (3.77 ± 1.42), Casey (3.12 ± 1.47) and Neumayer (2.38 ± 0.81), respectively. Unequal N HSD post hoc tests indicated that the Mawson and Davis CoFM values were similar ($P = 0.079$) while Neumayer and Drescher Inlet were different ($P < 0.0001$). Similarly, Kruskal–Wallis ANOVA also found significant differences between the six locations (Kruskal–Wallis test: $H(5, N = 836) = 123.9$, $P < 0.0001$). The Pearson Product Moment correlation between the CoFM and sample size per location was not significant ($r = 0.498$, $t = 1.148$, $P = 0.31$).

ANOVA results indicated a statistically significant difference in the mean frequency drop from start to end of the Trills between locations (All: $F(5, 831) = 73.635$, $P < 0.0001$; Mawson 1.59 ± 1.60 octaves, Davis 4.03 ± 1.64, Casey 2.83 ± 1.11, McMurdo Sound 3.74 ± 1.38, Neumayer 2.29 ± 0.74 and Drescher Inlet 4.28 ± 1.94). Unequal N HSD post hoc tests indicated that Mawson, Davis, Neumayer and Drescher Inlet were all significantly different from each other ($P < 0.024$). Many of the Trills at Mawson exhibited an initial drop of >1 octave but then began to increase in frequency; 29 of the 164 Trills ended at a higher frequency than they began. This pattern contributed to the lower mean frequency drop for the Mawson Trills. Mawson was the only base where any Trills ended at a higher frequency than they began.

Likewise, when examining the frequency drop between the first and second measure, ANOVA results indicated a statistically significant difference between locations (First pair: $F(5, 831) = 35.301$, $P < 0.0001$). Unequal N HSD post hoc tests indicated that Mawson (1.74 ± 1.17 octaves) differed from all other locations ($P < 0.0001$). The initial frequency drop at Neumayer (0.70 ± 0.59 octaves) was significantly less than that at Drescher inlet (1.21 ± 0.84: Unequal N HSD, $P = 0.0013$). The drops at Davis, Casey, and McMurdo Sound were 0.91 ± 0.87, 0.76 ± 0.68, and 0.59 ± 0.68 octaves, respectively.

The ranks of the means of the preceding features are presented in Table 2. The ranks of the means are independent of the validity of the statistical significance levels of the ANOVAs that may be associated with the absence of homogeneity of the variances. Cluster analysis of these ranks indicated that Casey and Neumayer were more similar to one another (linkage distance 5.0) than the Trills from the other locations. Mawson and Davis Trills were separated by a linkage distance of 7.9 while Neumayer and Drescher Inlet Trills were separated by the highest linkage distance 10.6.

k-means clustering, employing up to 30 clusters, failed to identify any Trill contour shapes that were unique to Casey or Neumayer. Conversely, although each of the other locations had a few unique contour shapes, the numbers were low and varied as the number of *k*-means clusters was increased from 6 to 30 (Fig. 3).

Except for Case where only 29% of the calls were correctly allocated, the General Discriminant Analysis classifications allocated 59–77% of the calls to the correct location (overall average 65.8%; Table 3). Many of the misclassified Trills were assigned to geographically distant locations and not the nearest neighbours. The canonical scores of the first two factors were plotted for the Mawson–Davis pair (Fig. 4a) and the Neumayer–Drescher Inlet pair (Fig. 4b). Ellipses that enclosed 50% of the data points are depicted in Fig. 4a, b and for all six locations in Fig. 5. Individual canonical scores from each of the six locations overlap each other. The 50% ellipses are presented in Fig. 5 to better depict the central groupings of the canonical scores of Trills from each of the geographic areas. Non-overlapping 50% ellipses of pairs of locations include Mawson–Davis, Mawson–McMurdo Sound, Mawson–Neumayer, Neumayer–Drescher Inlet and Newmayer–McMurdo Sound. Conversely, the 50% ellipse for Casey overlaps all of the other locations (Fig. 5). Within both the Mawson and Davis data sets, the distributions of the canonical scores for the different years exhibited slight variations. The centres of the distributions were all located within the respective ellipses shown in Fig. 4a.

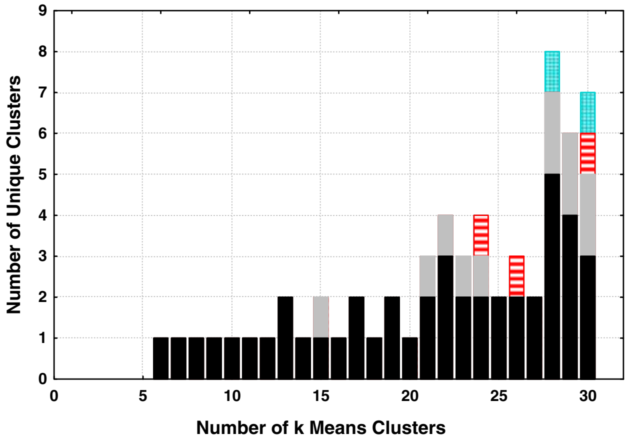
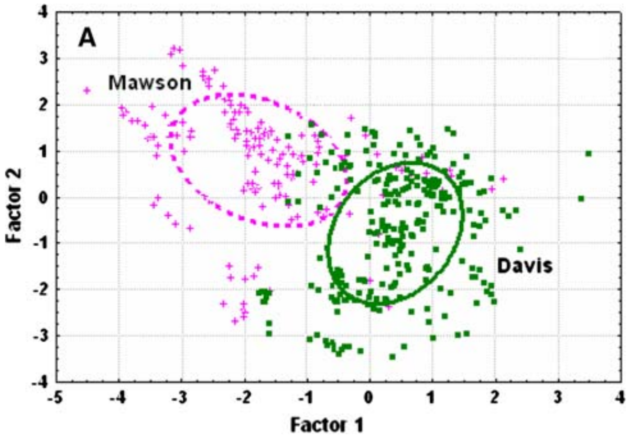


Fig. 3 Numbers of unique Trill frequency contour shapes per recording area as identified using different numbers of *k*-means clusters at Mawson Station (*solid black bars*), Davis Station (*grey bars*), McMurdo Sound (*horizontal bars*) or Drescher Inlet (*crosshatched bars*)

The Classification Trees analysis assigned 76.9% of the Trills to the correct location (Table 3). There were 21 terminal nodes. The Trills from Casey were not sufficiently distinctive to be classified correctly. Many of the misclassified Trills were assigned to geographically distant locations and not the nearest neighbours. When the data were analyzed using terminal node sizes of five, which results in increased splitting into smaller groups, the percent correct classification increased to 89.0%. When larger terminal nodes ($n = 40$) were used there were fewer groupings and

Table 3 Allocations of Weddell seal underwater Trills to the six recording locations using General Discriminant Analysis (GDA) and Classification Trees (CT, based on univariate splits)

Location	Trill Allocations (GDA/CT)					
	Mawson	Davis	Casey	McMurdo S	Neumayer	Drescher I.
Mawson	124/133	10/11	5/6	13/5	12/1	0/0
Davis	12/11	158/199.3	0/8	47/9.5	34/16.8	15/2.9
Casey	3/0	9/0.1	12/10.5	11/0	4/0	3/0
McMurdo Sound	14/13.9	17/28.1	1/8.8	114/136.2	2/6.5	13/8.1
Neumayer	1/1	8/10.5	5/2.4	5/4	70/65.4	2/2.1
Drescher Inlet	10/5.1	5/17	10/16.3	14/6.3	1/1.3	72/98.9
% Correct	76/81	59/75	29/25	71/84	77/72	64/88



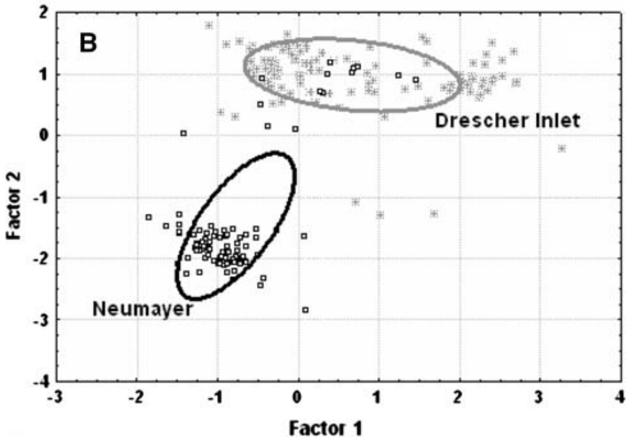


Fig. 4 Canonical scores obtained from a General Discriminant Analysis of the start and end waveforms (categorical values) and duration and eleven equally spaced frequency measures (continuous values) of Weddell seal underwater Trills recorded near (**a**) Mawson Station and Davis Station, or (**b**) Neumayer and Drescher Inlet, Antarctica. The ellipses enclose 50% of the data points from each location

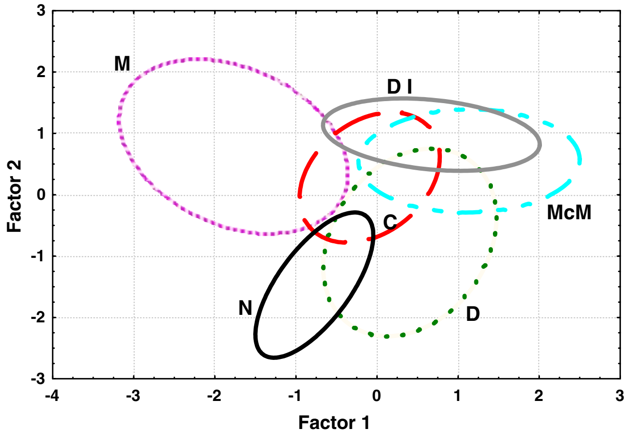


Fig. 5 Ellipses enclosing 50% of the canonical scores obtained from a General Discriminant Analysis of the start and end waveforms (categorical values) and duration and eleven equally spaced frequency measures (continuous values) of Weddell seal underwater Trills. Recording sites: M = Mawson, D = Davis, C = Casey, McM = McMurdo Sound. N = Neumayer and DI = Drescher Inlet

the correct classification dropped to 73.8% with no Casey calls correctly allocated.

Discussion

The two geographically closest recording locations, Neumayer and Drescher Inlet, exhibited the greatest differences in the Trill features (Table 2). Trill duration, start frequency, CoFM, ending waveform, overall frequency drop from start to end and frequency drop between the first and second measurement were all statistically different. Masking by leopard seal calls at McMurdo Sound and Drescher Inlet did not result in the disproportionate exclusion of Trills having low end frequencies. The mean end frequency of the Trills from these two locations were lower than those from all of the other recording locations except Davis (Table 2). Both the General Discriminant Analysis and the Classification Tree Analysis correctly identified the locations of the majority of the Trills from each recording area and a low proportion of the misclassifications were assigned to the nearest neighbour (Table 3). Although young Weddell seals have been observed to move between the Neumayer area at Atka Bay and Drescher Inlet, there is no evidence of clinal variation in the vocal patterns.

Similarly, the next two closest recording locations, Mawson and Davis, exhibited statistically significant differences in start frequency, end frequency, overall frequency drop from start to end and frequency drop between the first and second measurements (Table 2). The General Discriminant Analysis and the Classification Tree Analysis both identified the correct locations of the majority of the Trills from each recording area and a low proportion of the misclassifications were assigned to the nearest neighbour (Table 3). The distributions of canonical scores from the General Discriminant Analysis (first two factors) exhibit little overlap between the two recording locations (Fig. 4a). Mawson had the most distinctive Trill patterns of all the recording locations (Figs. 3, 5). The presence of Trills that rose in frequency towards the end was a major contributor to this distinctiveness. Mawson and Davis are located on opposite sides of Prydz Bay and there are no physical barriers between them. Nevertheless, there are no reports of Weddell seals tagged at Davis being sighted at Mawson (Abgrall et al. 2003) suggesting that male breeding site fidelity is high. The lack of evidence of clinal variation suggests that the Mawson and Davis Weddell seal groups have been separated for a long time.

The number of frequency contour shapes that were unique to one location varied directly with the number of *k*-means clusters (Fig. 3). However, there was no clear break point in the number of unique contours that would suggest an optimal number of *k*-means clusters to use in this type of analysis. Mawson and Davis exhibited the greatest proportion of unique frequency contours over the range of *k*-means clusters formed (Fig. 3). The rising frequency at the end of many Mawson Trills was distinctive, and sets this pattern apart from Trills recorded at all of the other locations. A few Trill frequency contour shapes from Davis were also distinctive, which further separates the Mawson and Davis Trill similarities. For the other recording locations, the differing numbers of *k*-means clusters produced inconsistent numbers of unique shapes per location. For example, the Drescher Inlet and McMurdo Sound Trill contour shapes were not very different from each other or the typical overall Trill patterns. Only one or two unique Trill shapes were identified at either of these locations and the mathematical derivation of the clusters often resulted in unique contours being identified at lower numbers of *k*-means clusters only to have them disappear when a higher number of clusters were formed (Fig. 3). The absence of unique frequency contour shapes at Casey and Neumayer suggests that Trills from these two bases all match common patterns.

Except for Casey, the General Discriminant Analysis correctly allocated most of the Trills to their correct location (Table 3). Both the Mawson–Davis pair and the Neumayer–Drescher Inlet pair had few misclassifications between pair members. The degree of similarity and variation among the Trills produced at the six locations is shown in Fig. 5. While there is a lot of overlap of data points between the locations, the general trends (denoted by ellipses enclosing 50% of the first two Factors of the canonical scores) indicate that Mawson Trills are well separated from those at Davis and the other locations. The between-years variation at Mawson and Davis was too slight to be significant. Similarly Neumayer Trills are well separated from the others (Fig. 5). The Classification Tree method yielded higher percent correct classifications than the General Discriminant Analysis but the patterns were similar (Table 3). Because the same data were used in both analyses, this similarity is to be expected. It does, however, point out that the different multivariate analysis methods do produce slightly different results and thus provide information on general trends but not precise values.

Although the majority of Trills from five of the six locations (exception Casey) were geographically distinct (Table 3), many acoustic features of the Trills overlap between areas. This is to be expected because of the general similarity of calls classified as Trills and their presumed common function. To human ears, the trills from the various locations sound different. For example, the Trills at Davis have predominately sinusoidal waveforms while those at McMurdo exhibit frequency modulation. Male and female Weddell seals are physically capable of producing a wide variety of calls which include both sinusoidal, frequency modulated and pulsed components (Thomas and Kuechle 1982; Terhune et al.1993). Thus it is unlikely that physiological limitations are shaping the differences in Trill structures between geographic areas.

Significant genetic differentiation between Weddell seal groups has been found at geographic distances of approximately 700 km. A “home” assignment analysis of 19 of 23 populations obtained from eight widely separated regions around Antarctica correctly allocated about 25% of individuals to their nominal region (Davis et al. 2008). Genetic distance between breeding colonies was significantly correlated to physical distance (Davis et al. 2008) but adjacent locations did not exhibit clinal variation. The four populations that were excluded from that analysis were strongly differentiated from all of the other groups and one of these occurred at each of Davis and McMurdo Sound. One of the three breeding groups at Davis and one of the seven breeding groups at McMurdo Sound were genetically distinct from adjacent groups that were <20 km away. At Davis, the vocal repertoires were not distinguishable between the various breeding groups (Pahl et al. 1997) although differences were found between Davis and Mawson (Abgrall et al. 2003). These findings coincide with observations from other species. Fin whales (*Balaenoptera physalus*) show no linear correlation between acoustic divergence and the geographic distance among sampled regions. Moreover, male fin whales that are genetically similar are more likely to sing different songs (Hatch and Clark 2004). A mechanism that could produce such a pattern is character displacement (Brown and Wilson 1956). Assuming this model for the evolution of the acoustic repertoire, patterns of variation in male song are mediated by strong selective pressures to differentiate under conditions in which calls could presumably attract mates from different populations or species (Bradbury and Vehrencamp 1998). As a result male calls are more likely to diverge in regions in which singers are sympatric, either physically or acoustically.

The Trills from Casey did not exhibit features that would distinguish them from Trills from the other five locations. The Casey sample size was the smallest but, for frequency measures at least, there was no correlation with sample size. Casey is the only one of the six locations that did not have a Trill feature that ranked highest or lowest (Table 2). This commonality of Trill features resulted in the high levels of misclassifications (Table 3). There is no apparent relationship with geographic distance in the overlap of the canonical scores of the other five locations (Fig. 5). The Trill call type is broadly defined (Thomas and Kuechle 1982; Oetelaar et al. 2003) and sampling at a location where the trill features exhibit average values could be due to chance.

The potential for oversampling a single individual was reduced at Mawson, Davis and Casey by randomly selecting only 10–20 calls per breeding group. The greater numbers of males at the larger breeding groups would also reduce the potential for oversampling . The variability of Trills within recording locations and the overlap with the other sites (Fig. 4a, b) suggest that a variety of males were sampled at each recording location or individual males may produce a variety of Trills. If males produced individually distinctive Trills that had features that were not similar to those of their immediate neighbours then the geographic patterns would not be evident.

A number of studies have demonstrated geographic variation in the structures and usage of underwater phocid calls (Thomas and Stirling 1983; Cleator et al. 1989; Thomas and Golladay 1995; Perry and Terhune 1999; van Parijs et al. 2003). Conversely, some distinct large phocid populations do not exhibit vocal differences, presumably through mixing (i.e., harp seals from the Front and Gulf herds: Perry and Terhune 1999). In the case of calls emitted by Weddell seals, previous studies have shown that breeding groups in close proximity (<130 km) to each other are not vocally differentiated (Pahl et al. 1997) while those a few hundred kilometres apart (Mawson and Davis in this case) can have very different call features (Abgrall et al. 2003). The types of multivariate statistical analyses used in geographical variation studies can vary greatly (e.g., Esterby et al. 2000), nevertheless the consistent finding is that underwater calls can be used as a natural tag to identify distinct groups within phocid species (Thomas and Stirling 1983; Cleator et al. 1989; Thomas and Golladay 1995; Perry and Terhune 1999; van Parijs et al. 2003). Where variation in vocal patterns within groups is less than that between groups, it is unlikely that the groups are interbreeding frequently.

Another possibility which cannot be tested using this data set is that relocated males, in a manner similar to some avian species, may change their Trills to match the local patterns (Lynch 1996). An advantage of this would be that the local females may be more likely to respond to familiar call patterns. The existence of Trills within a single location exhibiting very different frequency and waveform patterns suggests that learning is likely involved in Weddell seal vocal production. Assuming that the learning processes parallel the avian situation (Baptista 1996; Lynch 1996), males that remain near their birthplace throughout their lives would be exposed to local Trill patterns at an early age. Males begin making Trills as soon as the ice forms in early winter and juvenile seals share breathing holes with dominant males for months before the onset of the breeding season (Rouget et al. 2007). Thus there would be ample time for juvenile males to hear the Trill patterns that are common to that area before they reach sexual maturity and begin competing for dominance at breathing and breeding hole sites.

The site fidelity studies by Croxall and Hiby (1983), Cameron and Siniff (2004) and Cameron et al. (2007) covered ranges of <150 km along the coastline. There were occasional temporary influxes of immigrants from adjacent areas into these study areas under certain ice conditions (Cameron and Siniff 2004). Weddell seals tagged just after birth near Davis Station were likely observed ca. 150 km away at the Larsemann Hills (Pahl et al. 1997: seals bearing tags were seen but the researchers could not get close enough to read the tag numbers), but not ca. 630 km away at Mawson. The observation of Weddell seals tagged as pups and later being sighted ca. 500 km away in the Weddell Sea suggests that over time, long distance movements by Weddell seals are possible. The proportion of the population that moves significant distances away from their natal site is likely very low however. The establishment of geographic variation in underwater vocalizations between areas ca. 630 km apart, as reported for the entire vocal repertoire by Abgrall et al. (2003) or for a single male call type herein, suggests that adult Weddell seals are not interbreeding with adjacent groups of seals. If interbreeding were to occur, we would expect either clinal variation in the call patterns or a complete reduction of the geographic variation similar to that reported for harp seals in the Western Atlantic Ocean (Perry and Terhune 1999). It is likely that Weddell seals exhibit regional fidelity and never venture very far from their natal location.

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