

# Call Characteristics of High-Double Trill Leopard Seal (*Hydrurga leptonyx*) Vocalizations from three Antarctic Locations

by Cornelia M. Kreiss<sup>1</sup>, Olaf Boebel<sup>1</sup>, Horst Bornemann<sup>1</sup>, Lars Kindermann<sup>1</sup>, Holger Klinck<sup>2</sup>, Karolin Klinck<sup>2</sup>,  
Joachim Plötz<sup>1</sup>, Tracey L. Rogers<sup>3</sup> and Ilse C. Van Opzeeland<sup>1</sup>

**Abstract:** Leopard seals (*Hydrurga leptonyx*) produce underwater vocalizations during the breeding season in austral summer. Due to their solitary occurrence and remote habitat, hydroacoustic observations are an important technique to investigate this species regarding their population structure and acoustic ecology. This study examines, whether the acoustic characteristics of leopard seal high double trills (HDT) differed among three Antarctic locations (DI Drescher Inlet (72°52' S, 19°26' W), AB Atka Bay (70°31' S, 8°13' W) and DS Davis Sea (65° S, 90° E). Overall the observed pattern reflects a remarkable similarity in the acoustic characteristics of leopard seal HDTs across the three recording locations. Interestingly, differences in call characteristics were strongest between the closest sites DI and AB (500 km along-shelf-ice distance). HDTs recorded at DI had lower pulse repetition rates and narrower bandwidths than HDTs recorded at both, AB and DS (4300 km along-shelf-ice distance). Principal Component Analysis clearly separated HDTs recorded at DI from HDTs recorded at both, AB and DS. Calls from AB and DS were less separable and showed partly overlapping clusters. Previous genetic studies suggested that there is sufficient exchange of individuals between leopard seal breeding groups to prevent the development of genetically isolated populations. Our results support this notion as they demonstrate a high level of similarity in leopard seal vocalizations recorded at disparate locations. Subtle site variation in calls from recording locations within close proximity might be attributed to differences in local social factors including reproductive character displacement or environmental factors.

**Zusammenfassung:** Während der Aufzucht- und Paarungszeit im polaren Sommer zeigt der Seeleopard (*Hydrurga leptonyx*) eine hohe akustische Aktivität. Aufgrund ihres schwer zugänglichen Lebensraums und der solitären Lebensweise, stellen hydroakustische Untersuchungen eine wichtige Methode zur Erforschung dieser Spezies und ihrer akustischen Ökologie dar. In der vorliegenden Studie wurde eine Detailanalyse der Seeleoparden-Vokalisation „high double trill“ (HDT) in Hinblick auf geografische Unterschiede zwischen drei antarktischen Standorten (DI Drescher Inlet 72°52' S, 19°26' W, AB Atka Bucht 70°31' S, 8°13' W und DS Davis Sea 65° S, 90° E) durchgeführt. Die Mehrheit der akustischen Parameter des HDT zeigte eine deutliche Ähnlichkeit zwischen den drei Aufnahmestationen. Interessanterweise wichen die HDT Charakteristika der geografisch am nächsten gelegenen Stationen DI und AB am meisten voneinander ab (500 km entlang der Eisgrenze entfernt). HDTs der Aufnahmestation DI zeigten niedrigere Puls-Wiederholungsraten sowie schmalere Frequenzbandbreiten im Vergleich zu den HDT Aufnahmen von AB und DS (4300 km entlang der Eisgrenze entfernt). Eine Hauptkomponentenanalyse bestätigte die Abgrenzung der DI HDTs von denen der anderen beiden Stationen. Die Vokalisationen von AB und DS zeigten teilweise überlappende Cluster und konnten somit nicht klar separiert werden. Wie vorangegangene Studien zeigen, besteht zwischen Seeleoparden-Populationen genügend Austausch um eine genetische Struktur zu verhindern. Die Ergebnisse der vorliegenden Studie bestätigen diese Annahme im Hinblick auf die Ähnlichkeit der Vokalisation zwischen den beiden entferntesten Aufnahmestationen. Variation zwischen den HDTs der nahe gelegenen Untersuchungsgebiete weist auf soziale Faktoren wie z.B. Merkmalsverschiebung zur Verringerung interspezifischer Konkurrenz oder standortbedingte Anpassungen hin.

## INTRODUCTION

Acoustic signals mediate mate choice, resource defence and species recognition in a broad range of taxa with intraspecific geographic variation in these vocal signals occurring in many species (JANIK 2009, WILKINS et al. 2013). Patterns of geographic variation in communicating systems can provide insight into the process that drives phenotypic evolution (CAMPBELL et al. 2010), occurring for reasons of genetic variation or isolation (founder effect) or evolve due to processes of social learning or an adaptation to environmental conditions (e.g., HUNTER & KREBS 1979, CATCHPOLE & SLATER 1995, VAN PARIJS et al. 2003). Thereby, sexual selection has been proposed as the primary driver of acoustic divergence between populations (WILKINS et al. 2013). Especially bird vocalizations (passerines, psitticines and trochilids) express significant geographic variation, which can largely be attributed to their vocal learning through imitation (PODOS & WARREN 2007). However, the ability to copy complete new sounds is also known in some marine mammals (JANIK & SLATER 1997) and several phocid species exhibit geographic variation in their vocal behaviour, which in most species has been attributed to reproductive isolation of populations (e.g., LE BOEUF & PETERSON 1969, THOMAS & STIRLING 1983, PERRY & TERHUNE 1999, VAN PARIJS et al. 2003, RISCH et al. 2007, TERHUNE et al. 2008). PERRY & TERHUNE (1999) compared harp seal (*Pagophilus groenlandicus*) underwater vocalizations among three North Atlantic breeding locations (Gulf of St. Lawrence: 'Gulf', Front ice east of Labrador: 'Front' and Jan Meyen Island: 'Jan Mayen') and found the call repertoire and proportional call type usage in Gulf and Front (c. 500 km apart) to differ in a similar manner from the more distant Jan Mayen breeding group (c. 3500 km from the Gulf and Front). These findings are supported by tagging studies, which showed that the Gulf and Front herd interbreed and are reproductively isolated from the Jan Mayen herd. In Weddell seals, both the call repertoire and the acoustic characteristics of call types were found to differ on a mesogeographic (600–2000 km) and macrogeographic level (>2000 km), suggesting that breeding groups were unlikely to mix over these distances (ABGRALL et al. 2003, THOMAS & STIRLING 1983). On a microgeographic scale (150 km) no consistent differences existed in call repertoire and call characteristics between breeding groups (PAHL et al. 1997). These findings were also supported by tagging data, indicating that animals exhibited pronounced breeding site fidelity and moved only between nearby breeding locations (STIRLING 1974, PAHL et al. 1997, CAMERON et al. 2007).

<sup>1</sup> Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 26, 27568 Bremerhaven, Germany, Corresponding author <Cornelia.Kreiss@awi.de>

<sup>2</sup> Oregon State University, Cooperative Institute for Marine Resources Studies, Hatfield Marine Science Center, 2030 Marine Science Drive, Newport, OR 97365, USA.

<sup>3</sup> Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia.

Leopard seals (Fig. 1) are known to produce at least 13 different underwater vocalization types, which have been recorded during the breeding season from November to January (STIRLING & SINIFF 1979, THOMAS & GOLLADAY 1995, ROGERS et al. 1996, SOUTHWELL et al. 2003). The leopard seal call repertoire consists of short-distance “local calls” as well as long-distance “broadcast calls” (ROGERS et al. 1996). Broadcast call types that have been recorded from free-ranging leopard seals at various recording sites are: the high, medium and low double trill, medium single trill, hoot, hoot with single trill, and the low ascending and descending trill (STIRLING & SINIFF 1979, THOMAS & GOLLADAY 1995, ROGERS et al. 1996, KLINCK 2008). The HDT is a broadcast call known to be produced by both sexes and by juvenile and adult leopard seals (ROGERS et al. 1996, ROGERS 2007). A previous study showed that the HDT forms a relatively constant portion of the vocal repertoire of leopard seals over the period that they are vocally active (VAN OPZEELAND et al. 2010). HDTs have been found to be produced by leopard seals at all breeding sites studied to date (STIRLING & SINIFF 1979, THOMAS & GOLLADAY 1995, ROGERS et al. 1996, KLINCK 2008). The HDT is composed of two series (~3.5 s duration each) of short duration pulses (ROGERS et al. 1995). In contrast to the low double trill, which forms the largest portion of the leopard seal vocal repertoire (VAN OPZEELAND et al. 2010) the acoustic characteristics of the HDT allow reliable detection of this call type, even at

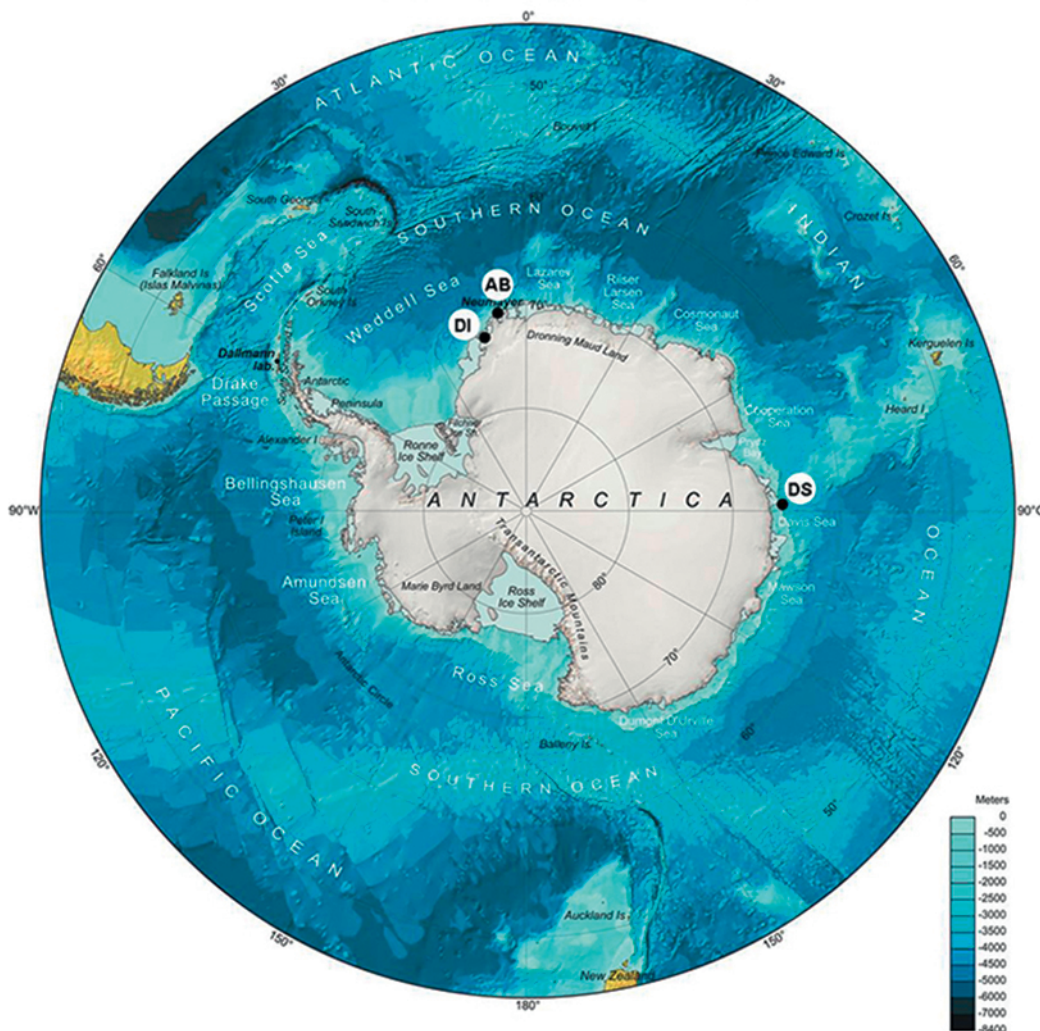


**Fig. 1:** Leopard seal (*Hydrurga leptonyx*) hauled out, Potter Peninsula, King George Island, Antarctica (© H. Bornemann).

**Abb. 1:** Seeleopard (*Hydrurga leptonyx*) an Land auf Potter-Halbinsel, King George Island, Antarktis (© H. Bornemann).

higher background noise levels (KLINCK 2008), and circum-polar comparisons of this call’s characteristics.

Leopard seals have a circumpolar distribution around the Antarctic continent between 50° S and the continental ice shelf. The main population occurs within the circumpolar



**Fig. 2:** Map of Antarctica showing the three study sites: DI = Drescher Inlet, AB = Atka Bay, and DS = Davis Sea. Cartography: D. Graffe, Alfred Wegener Institute. Modified from: IOC, IHO and BODC (2003).

**Abb. 2:** Übersichtskarte der Antarktis mit den drei antarktischen Untersuchungsgebieten: DI = Drescher Inlet, AB = Atka Bucht und DS = Davis Sea. Kartographie: D. Graffe, Alfred Wegener Institut; modifiziert nach: IOC, IHO und BODC (2003).

pack ice, with higher densities near the pack ice (e.g., KING 1983, SINIFF 1991, BESTER et al. 2002). Migration from pack ice to the Subantarctic islands during winter was observed mainly for subadult animals (SINIFF & STONE 1985), while migration patterns of adults remain largely unknown. Hence, the current knowledge on leopard seal breeding populations and their mixing and distribution is sparse. SLIP et al. (1994) and DAVIS et al. (2008) found the genetic diversity in leopard seals, sampled at several circumpolar locations, to be low, suggesting that there is at least sufficient gene flow between breeding groups to prevent the development of genetic differentiation between populations. THOMAS & GOLLADAY (1995) compared leopard seal underwater vocalizations between McMurdo Sound and Palmer Peninsula (separated by c. 5000 km), and found significant differences in call repertoire and call characteristics. They suggested that repertoires are likely to vary slightly between adjacent areas, and be more distinctive between distant regions, reflecting the low probability of encounter between geographically separated breeding groups. Hence, insights into the patterns of geographic variation of vocal behaviour could potentially reveal more about the discreteness of leopard seal groups and the pattern of mixing among populations or breeding groups. In this study we compare leopard seal vocal behaviour between three Antarctic locations, Atka Bay, Drescher Inlet and Davis Sea (Fig. 2), which allows comparisons on two different spatial scales: Atka Bay and Drescher Inlet have an along-shelf-ice distance of approximately 500 km, whereas the distance between Atka Bay and Davis Sea is about 4300 km. Drescher Inlet and Davis Sea have an along-shelf-ice distance of 4800 km.

## METHODS

### Data collection

Davis Sea data: Acoustic data from Davis Sea (DS, Fig. 3) were collected during an acoustic survey of the RV “Aurora Australis” V4. Recordings were made on 13 to 14 December 1997 (12 hours) on six locations between 62° S, 93° E and 63° S, 90° E. Water depth at these locations ranged from 3600–4000 m and ice cover at these locations varied between 40 % and 80 %. Recordings were made remotely using a sonobuoy (Sparton Electronics AN/SSQ-57A: frequency response 10 Hz - 20 kHz). Hydrophones were lowered to a depth of 18 m below the water surface. Signals were received with a custom-built receiver and recorded onto a Sony Digital Audio Tape recorder (TCD-D8: frequency response 10 Hz–22 kHz).

Drescher Inlet data: During the Drescher Inlet Pilot Study (DIPS) acoustic recordings were made from 17 December 2003 to 2 January 2004 in the Drescher Inlet (DI) (Fig. 4). At that time DI was located at 72°50' S, 19°02' W, forming a 25 km long and up to 2 km wide crack in the Riiser Larsen Ice Shelf. The seabed under the ice shelf extends over 100 km to the nearest grounding line of Dronning Maud Land (SCHENKE et al. 1998). The recording setup was placed on solid sea ice at a distance of about 6 km from the sea ice edge. Three RESON TC4032 hydrophones were deployed through boreholes in a 100 m baseline triangle at 100 m water depth. Effective bandwidth of the recordings is 10 Hz to 24 kHz. Acoustic recordings from 21 to 25 December 2003 (86 hours) were included in this study.



**Fig. 3:** Leopard seal (*Hydrurga leptonyx*) hauled out on ice floe within Prydz Bay, Davis Sea, Antarctica (© T. Rogers).

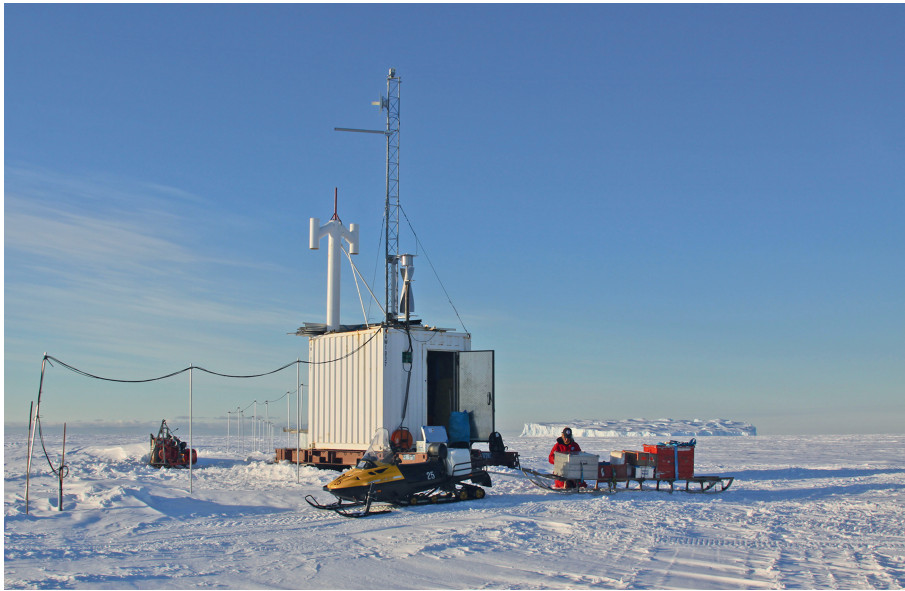
**Abb. 3:** Seeleopard (*Hydrurga leptonyx*) auf einer Eisscholle in der Prydz-Bucht, Davis Sea, Antarktis (© T. Rogers).



**Fig. 4:** Mobile ice-camp on Riiser Larsen Ice Shelf for acoustic observation within the Drescher Inlet (72°50' S, 19°02' W), a 25 km long and 2 km wide crack in the Ice Shelf (© J. Plötz).

**Abb. 4:** Mobiles Eiscamp auf dem Riiser Larsen Schelfeis zur Aufnahme von Unterwasservokalisationen innerhalb des Drescher Inlet (72°50' S, 19°02' W), einem 25 km langen und 2 km breiten Riss im dortigen Schelfeis (© J. Plötz).

Atka Bay (PALAOA) data: Underwater recordings from Atka Bay (AB) were obtained from the PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA; Fig. 5). PALAOA is an autonomous acoustic observatory located at 70°31' S, 8°13' W on the Eckström Ice Shelf, 16 km north of the German Antarctic station Neumayer III. AB is covered with fast-ice from March to January. For this study, recordings were made with a RESON TC4032 hydrophone located underneath the 100 m thick floating Eckström Ice Shelf, 80 m below the ice shelf (BOEBEL et al. 2006, KLINCK 2008). Effective bandwidth of the recordings is 10 Hz to 16 kHz. Previous analysis of the PALAOA data showed a peak in leopard seal calling activity towards the end of December (VAN OPZEELAND et al. 2010), which has also been reported by previous studies (THOMAS & DEMASTER 1982, ROGERS et al. 1996). Acoustic recordings included in this analysis were extracted from the period 21 to 27 December 2006 (156 hours).



**Fig. 5:** The autonomous acoustic observatory PALAOA (Perennial Acoustic Observatory in the Antarctic Ocean) located at 70°31' S, 8°13' W on the Eckström Ice Shelf, 16 km north of the German Antarctic station Neumayer III; top = View towards North and Southern Ocean with iceberg grounded just beyond the ice shelf break (© C. Kreiß); bottom = View from Atka Bay (© AWI).

**Abb. 5:** Die autonome akustische Aufnahmestation PALAOA (Perennial Acoustic Observatory in the Antarctic Ocean) auf dem Eckström Schelfeis (70°31' S, 8°13' W), 16 km nördlich der deutschen Forschungsstation Neumayer III; oben = Blick nach Norden auf Südlichem Ozean mit kurz hinter der Schelfeiskante auf Grund gelaufenem Eisberg im Hintergrund (© C. Kreiß); unten = Sicht aus der offenen Atka Bucht (© AWI).

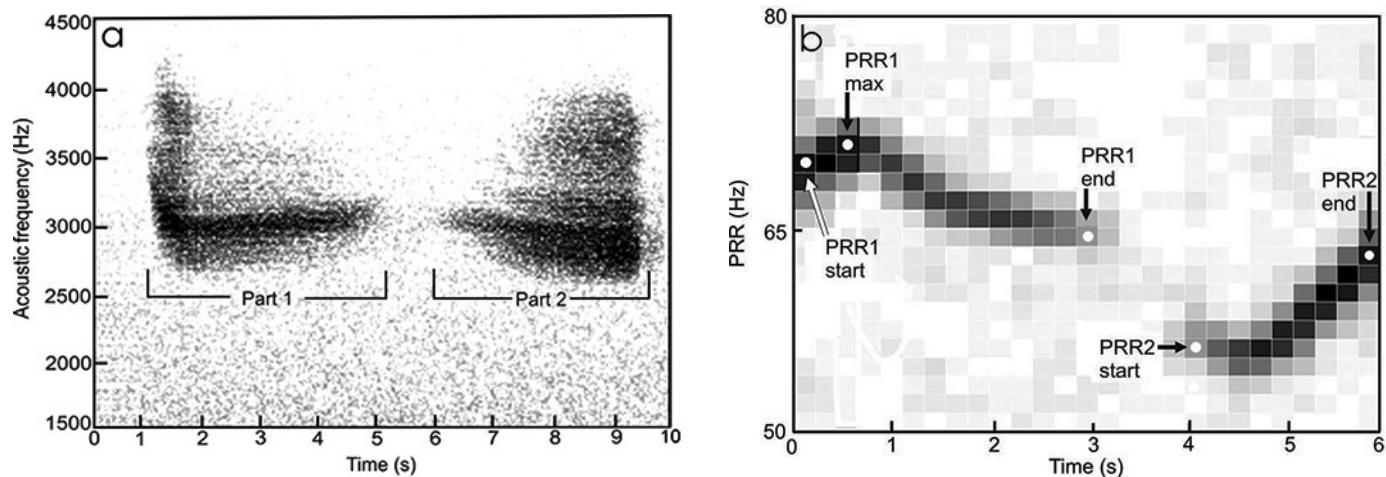


### Data analysis

For each location, 150 HDTs (Fig. 6a) with a band-limited (1.5 - 4.5 kHz) signal-to-noise ratio > 10 dB were selected for further analyses. In total 63 acoustic parameters were measured for all 450 HDT samples and investigated for differences. Using 'Osprey', a noise-robust 'Matlab'-based analysis software, 29 generic acoustic parameters were extracted from each of the two parts of the HDT calls. For this analysis the following spectrogram parameters were used: frame size and FFT size 4096 samples (0.085 s), overlap 50 % (0.043 s), and Hamming window, for a spectrum filter bandwidth of 47.6 Hz. A detailed description of how 'Osprey' determines the 'feature box' as well as a detailed description of all 29 parameters and how they are calculated are given by MELLINGER & BRADBURY (2007).

The remaining five acoustic parameters describe the temporal evolution of the pulse repetition rate (PRR). The PRR is the rate of amplitude modulation of the signal, which is reflected in the spectrogram by sidebands of the carrier frequency

(KLINCK et al. 2008). Parameters of the PRR measured were (Fig. 6b): start PRR of call part 1, maximum PRR of call part 1, end PRR of call part 1, start PRR of call part 2, end PRR of call part 2. For a more detailed description of how the PRR parameters were measured, see KLINCK et al. (2008). To visualize the distribution of each acoustic parameter, we used the 'Matlab' Statistics Toolbox to produce estimates of 'probability density functions' (PDFs) of all parameters for each geographic location. First, the parameter space (min to max) was linearly interpolated to 100 steps for each location. Second, PDFs were calculated using the 'Matlab' function 'ksdensity', employing a normal kernel distribution of optimized width (default settings, see 'Matlab' function description). Figures 7a-d exemplify the results for the parameters call duration, bandwidth, pulse repetition rate and signal-to-noise ratio of call part 1. The full set of parameter PDFs were screened for parameters irrelevant to the further analysis on spatial variability. Parameters without notable spatial dependency and those defining the 'Osprey' analysis window were excluded from the subsequent analysis. All remaining acoustic



**Fig. 6:** (a) = Spectrogram of the high double trill; (b) = Spectrogram of the high double trill modulation frequencies: PRR1 start = PRR start of call part 1; PRR1 max = PRR maximum of call part 1; PRR1 end = PRR end of call part 1; PRR2 start = PRR start of call part 2; PRR2 end = PRR end of call part 2.

**Abb. 6:** (a) Spektrogramm des „high double trill“; (b) = Spektrogramm der Modulationsfrequenzen des „high double trill“: PRR1 start = PRR zu Beginn von Vokalisationsteil 1; PRR1 max = maximale PRR von Vokalisationsteil 1, PRR1 end = PRR zum Ende von Vokalisationsteil 1; PRR2 start = PRR zu Beginn von Vokalisationsteil 2; PRR2 end = PRR zum Ende von Vokalisationsteil 2.

parameters were included in a Principal Component Analysis (PCA) to explore acoustic separability of HDTs according to recording location.

## RESULTS

The mean duration of call part 1 was  $1.10 \pm 0.53$  s (mean  $\pm$  standard deviation) for DS and  $1.22 \pm 0.61$  s for AB, while the recordings from DI showed an intermediate mean duration of  $1.17 \pm 0.48$  s (Tab. 1). Call part 2 showed a corresponding pattern in mean duration for the three study sites, but had generally shorter durations compared to call part 1.

Kernel density estimations for the durations of leopard seal HDTs at the three study sites show largely overlapping distributions for call part 1 (Fig. 7a). The curves are positively skewed, showing a peak for short call durations and an elongated tail towards longer call durations.

For lower and upper frequencies of the HDT, calls from DI had substantially higher values for lower frequencies and lower values in upper frequencies compared to the other two sites. The mean lower frequency of call part 1 for DI was approximately 100 Hz higher compared to AB and 80 Hz higher compared to DS (Tab. 1). The mean for upper frequencies of call part 1 was approximately 600 Hz lower for high double trills recorded at DI compared to DS and more than 100 Hz lower as for HDTs recorded at AB. The resulting mean bandwidth of the calls at DI was substantially narrower than those of HDTs recorded at AB and DS (Tab. 1). However, as the SNRs were lowest at DI compared to the other study sites (Fig. 7d, Tab. 1), observed bandwidths might also be influenced by local SNRs, rather than being signal specific.

Interestingly, kernel density estimates revealed bimodal distributions of the bandwidths of call part 1 for AB (green, Fig. 7b) and DS (blue), overlapping partly with DI (red). The results for call part 2 showed a corresponding pattern for the means of lower and upper frequencies between the three locations,

though with smaller differences between locations than call part 1.

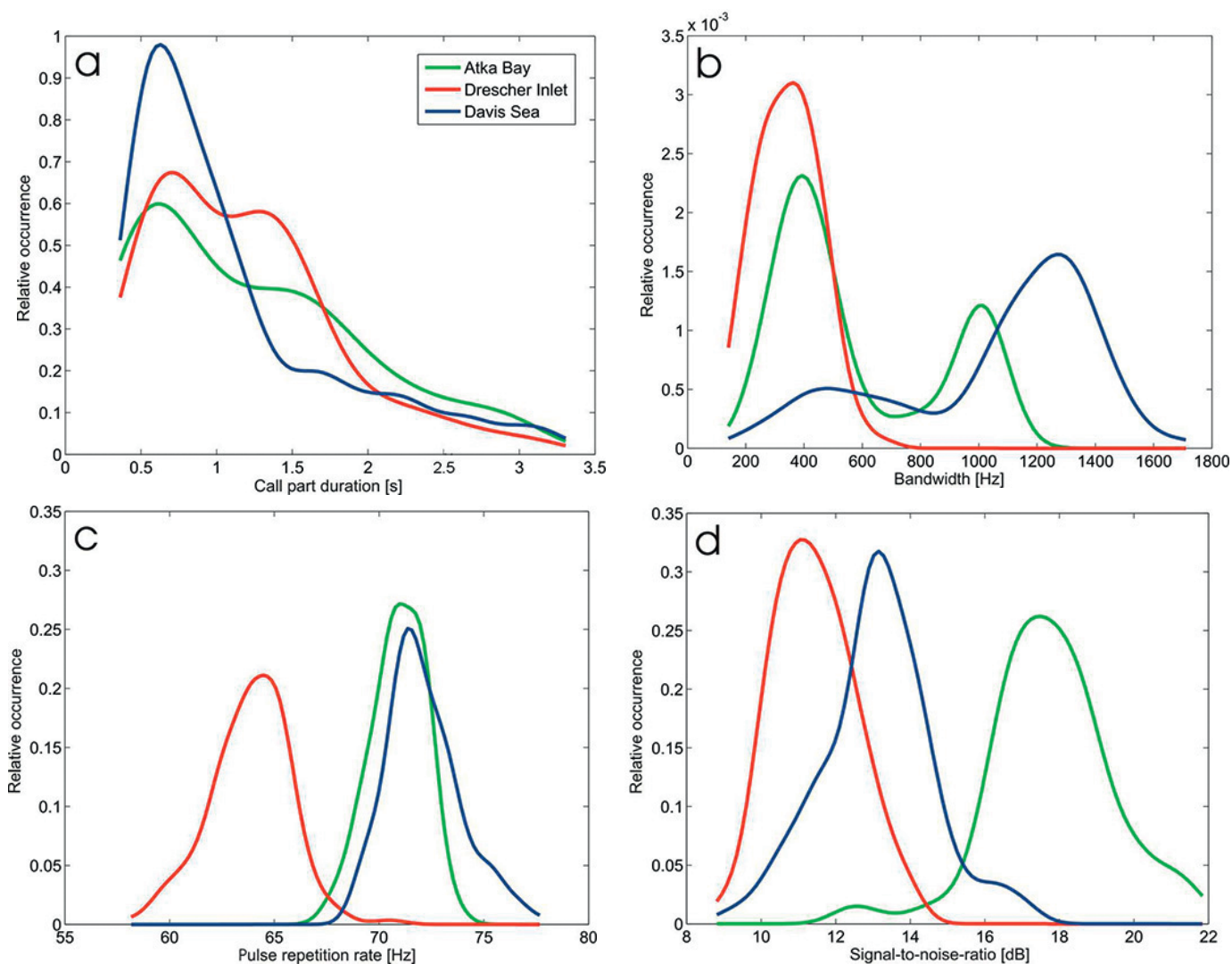
All PRR values measured for HDTs recorded at DI (Fig. 7c, red) were lower than PRR values of calls recorded at AB (green) and DS (blue), respectively (Tab. 1). The distributions of the five pulse repetition rate parameters clearly separated DI from AB and DS calls. Calls from DI generally tended towards lower PRR which was most distinctive in the PRR start of call part 1 (Fig. 7c). PRR values measured for call part 2 showed a similar trend as call part 1, although differences between DI and the other two locations were less pronounced.

To explore if calls could be separated according to recording location, we performed a Principal Component Analysis (PCA). As described previously, only a subset of the relevant acoustic parameters was included in the PCA. These were all five PRR parameters, the lower and the upper frequency and the duration of call part 1 and 2. The first two principal components of the PCA explained 67 % of the variance (Tab. 2) and revealed a clear separation of the HDTs originating from DI from those recorded at the other two study sites (Fig. 8). Component 1 represents mainly the contribution of the PRR parameters, whereas component 2 reflects the importance of the upper frequency of both call parts in distinguishing locations (Tab. 1).

## DISCUSSION

### *Variation between recording sites*

The results of our study reveal notable differences in the acoustic features of leopard seal HDTs recorded at the three different sites. The PCA clearly separated Drescher Inlet HDTs from those of Atka Bay and Davis Sea, suggesting that local environmental conditions and social factors are more influential on HDT call characteristics than large scale geographical separation. Davis Sea and Atka Bay HDTs were inseparable with regard to the first PCA component, yet differed at least to some extent with regard to the second.



**Fig. 7:** Kernel density estimations for (a) = duration, (b) = bandwidth, (c) = pulse repetition rate, and (d) = signal-to-noise ratio of call part 1 of high double trills recorded at Atka Bay = green, Drescher Inlet = red, and Davis Sea = blue.

**Abb. 7:** Kerndichteschätzung der Dauer = (a), Frequenzbandbreite = (b), Puls-Repetitionsrate = (c) und des Signal-zu-Rausch Verhältnisses = (d) von Vokalisationsteil 1 des „high double trill“, aufgenommen in der Atka Bucht = grün, dem Drescher Inlet = rot und der Davis Sea = blau.

For individual call characteristics, differences were more pronounced between the closest sites (DI *versus* AB, 500 km apart) and the least, between the most disparate sites (AB and DS, 4300 km). The bandwidth and pulse repetition rates of calls recorded at DI differed from calls recorded at AB and DS, whereas calls recorded at the latter two locations were not clearly separable according to recording site. However, overall the observed pattern reflects a remarkable similarity in the acoustic characteristics of leopard seal HDTs across the three recording locations. While other species, such as harp and Weddell seals, exhibit considerable variation in their vocal behaviour between breeding groups on varying spatial scales (e.g., PERRY & TERHUNE 1999, ABGRALL et al. 2003), our measurements show that leopard seal HDTs exhibit substantial acoustic similarity up to a spatial scale of 4300 km. All studies (this and those quoted above) analysed acoustic data recorded during each species respective breeding season, implying that calls might be used for mate attraction.

However, it must be taken into account that the present study is based on only one call type, whereas variation in

harp and Weddell seal vocalizations was based on the entire vocal repertoire. Nevertheless, our results indicate that there is mesogeographic (500 km) rather than macrogeographic (4300 km) variation for the HDT leopard seal vocalizations. In contrast, THOMAS & GOLLADAY (1995) suggested leopard seal vocalizations to vary clinally. For a further understanding of these patterns genetic and tagging data have to be considered. DAVIS et al. (2008) found no genetic differentiation between leopard seal populations across the Antarctic and suggested that there is sufficient gene flow between breeding groups to prevent development of population structure. Further information on movement patterns obtained from tagged leopard seals does not exclude exchange of or contact between individuals from different breeding locations, although the range of movement varies largely between individuals (ROGERS et al. 2005, NORDØY & BLIX 2009).

Therefore, acoustic similarity found in our study likely mirrors exchange or at least contact between individuals from the three different recording locations and suggests that subtle site differences are attributable to other factors than geogra-

	AB		DI		DS	
	Mean	Std. deviation	Mean	Std. deviation	Mean	Std. deviation
Lower frequency part 1 [Hz]	2807.08	41.58	2919.11	34.92	2836.89	33.85
Upper frequency part 1 [Hz]	3391.99	264.15	3264.62	74.70	3889.36	301.26
Bandwidth part 1 [Hz]	584.91	252.95	345.51	88.76	1052.47	291.21
Lower frequency part 2 [Hz]	2741.7	35.0	2849.7	42.5	2794.4	30.5
Upper frequency part 2 [Hz]	3220.9	196.9	3192.0	75.8	3557.1	324.5
Duration part 1 [s]	1.22	0.61	1.17	0.48	1.10	0.53
Duration part 2 [s]	1.03	0.20	1.01	0.23	0.93	0.25
Signal-to-noise ratio part 2 [Hz]	17.8	1.2	11.4	0.9	13.1	1.1
PRR start part 1 [Hz]	70.92	0.98	63.84	1.43	72.15	1.38
PRR max. part 1 [Hz]	74.93	0.65	68.55	0.89	76.00	1.40
PRR end part 1 [Hz]	70.53	1.63	62.82	1.66	72.04	2.12
PRR start part 2 [Hz]	64.45	2.66	57.21	2.01	63.68	2.75
PRR end part 2 [Hz]	72.25	0.88	66.68	1.40	70.37	1.40

**Tab. 1:** Descriptive statistics of selected acoustic parameters measured for leopard seal high double trills (HDT) recorded at Atka Bay (AB), Drescher Inlet (DI) and Davis Sea (DS); n = 150 for each location.

**Tab. 1:** Beschreibende Statistik ausgewählter akustischer Messparameter des Seeleoparden „high double trill“ (HDT), aufgenommen in der Atka Bucht (AB), dem Drescher Inlet (DI) und der Davis Sea (DS), n = 150 für jede Aufnahmestation.

	PC1 [49 %]	PC2 [18 %]	PC3 [11 %]
PRR start part 1	0.40	-0.01	0.14
PRR max part 1	0.40	0.00	0.17
PRR end part 1	0.40	0.13	-0.08
PRR start part 2	0.37	0.00	-0.32
PRR end part 2	0.36	-0.20	-0.06
Lower frequency part 1	-0.32	0.32	0.02
Upper frequency part 1	0.20	0.49	0.33
Duration part 1	-0.07	-0.40	0.56
Lower frequency part 2	-0.28	0.35	-0.11
Upper frequency part 2	0.14	0.53	0.38
Duration part 2	-0.10	0.21	0.50

**Tab. 2:** Component loadings from Principal Component Analysis parameters measured for HDTs recorded at Atka Bay, Drescher Inlet and Davis Sea; n = 150 for each location.

**Tab. 2:** Faktorladungen der Komponenten aus der Hauptkomponentenanalyse der HDTs, aufgenommen in der Atka Bucht, dem Drescher Inlet und der Davis Sea; n = 150 für jede Aufnahmestation.

phic isolation of populations. Leopard seals vocalizations revealing variation between locations 5000 km apart (THOMAS & GOLLADAY 1995) might also be explained by factors other than geographic isolation. While in non-migratory species or species that show site fidelity, geographic variation in vocal behaviour in some cases reflects distinct breeding populations or subpopulations (e.g., NELSON et al. 2001, STAFFORD et al. 2001, ABGRALL et al. 2003) for species who display contact

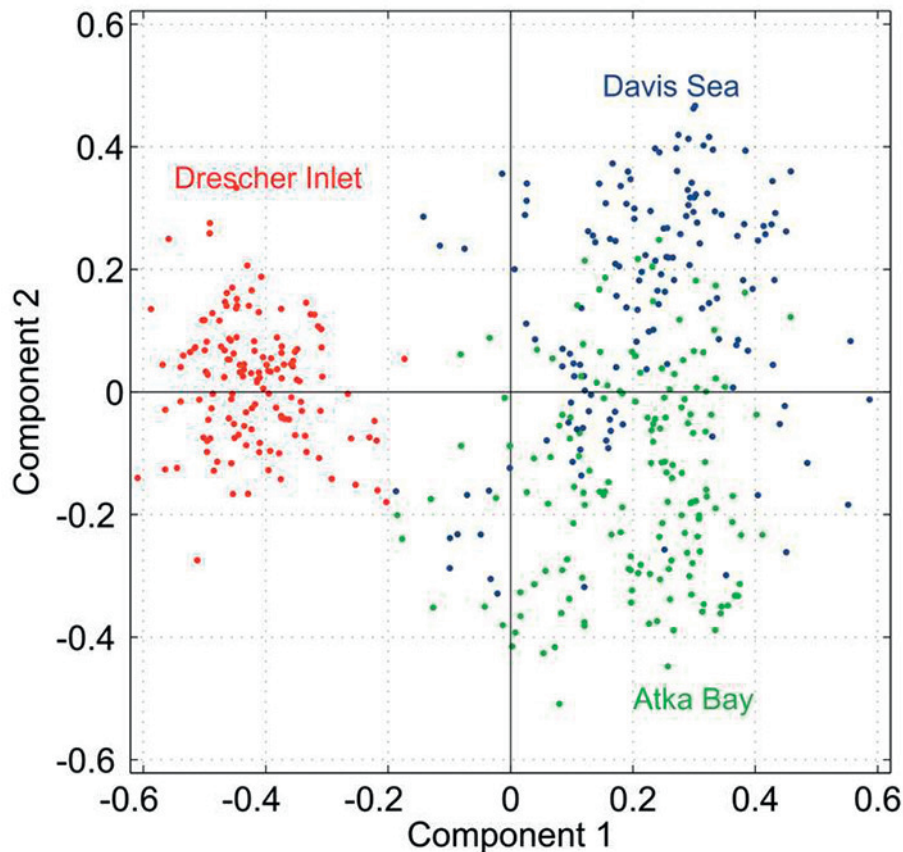
between different breeding groups acoustic and population mixing behaviour should be investigated.

Below we further discuss various aspects that might explain the observed differences in call characteristics between DI versus AB and DS, recognizing that these might also act in concert.

#### *Differences in local group composition and temporal variation*

In our study there was no explicit information on the number of individuals present and likely only a relatively small number of individuals may have been sampled acoustically. However, overlapping calls in the DS data set suggest that more than one animal was sampled, and when taking the leopard seals' territorial behaviour into account it is likely that multiple animals were recorded at the spatially separated six recording locations in DS. Referring the high call frequency of 8.9 calls per minute at AB and 5.6 calls per minute at DI (KLINCK 2008) to earlier reported mean calling rates for individual male leopard seals (ROGERS 2007) let assume that at least two animals were recorded at these two sites.

Adult male leopard seals within a region show only little difference between acoustic characteristics for the HDT call with no detectable clustering on individual level (ROGERS & CATO 2002). Therefore, vocalizations of even few individuals are likely to represent the acoustic characteristics of a local population. There was also no information on the sex or age class of callers, consequently it is not known to what extent differences in group composition between the three localities may have influenced the results. The acoustic characteristics of the HDT are known to differ substantially between leopard



**Fig. 8:** Scatterplot of the first two principal components of a PCA applied on all pulse repetition rate parameters, upper and lower frequency and duration of both call parts extracted from 450 HDTs recorded at Drescher Inlet (red), Atka Bay (blue) and Davis Sea (green).

**Abb. 8:** Streudiagramm der ersten beiden Hauptkomponenten der Hauptkomponentenanalyse, angewandt auf alle Parameter der Puls-Repetitionsrate, der obersten und untersten Frequenz, sowie die Dauer beider Vokalisationsteile. Diese wurden aus 450 HDTs extrahiert, aufgenommen in der Atka Bucht (grün), dem Drescher Inlet (rot) und der Davis Sea (blau).

seals of different age classes (ROGERS et al. 1996, ROGERS 2007). In our data, HDT bandwidths of calls recorded at AB and DS were found to have a bimodal distribution, possibly reflecting two ‘types’ of HDTs produced by different age classes and/or sexes. (Explaining this bimodality by varying distances of animals to the hydrophone, and hence varying SNRs, appears unlikely, as the bimodality observed in the bandwidths is not reflected in the SNR, cf. Figs. 7b & 7d). In addition, the absence of this bimodal pattern and partial overlap of distributions of AB and DS with DI suggests calls (and potentially group position) are more homogeneous at the latter location. Considering that this pattern was not found for pulse repetition rate this might be a more robust parameter being independent of age-related differences. It cannot be excluded that the differences in leopard seal call repertoire and call characteristics between Palmer Peninsula and McMurdo Sound reported by THOMAS & GOLLADAY (1995) can be attributed to differences in local group composition, given that in their study no information on the individuals that produced the calls was collected either.

The lack of information on the age and sex of the individuals that produced the HDTs in our study is an aspect of our data, which we share with many other studies investigating the underwater vocalizations of marine mammals (e.g., PERRY & TERHUNE 1999, STAFFORD et al. 2001, ABGRALL et al. 2003, ROSSI-SANTOS & PODOS 2006, MAY-COLLADO & WARTZOK 2008). Although in many cases such information can simply not be collected due to the fact that callers are submerged most of the time and/out of the sighting range, awareness of this potential bias can overcome over-interpretation of site variation in vocalizations. Particularly in territorial species

(i.e., species that defend geographic underwater areas against rival individuals), which likely also includes the leopard seal, acoustic sampling should be conducted with caution e.g., by recording at several locations to ensure that calls of a sufficiently large number of individuals are sampled.

Despite vocal signals possibly varying on a geographic scale, differences might also be due to temporal variation. In the present study especially the temporal difference of nine years between vocal signals recorded at DS (1997) and AB (2006) might have a significant effect of the results. However these two sites showed the highest similarity within the three study locations, while acoustic data from DI recorded in between (2003) revealed diverging call characteristics mostly from those of AB. We conclude that at least no linear temporal variation was present in our data.

#### *Local environmental conditions*

Recordings from DI featured lowest signal-to-noise ratio of all three sites. Leopard seals use their calls to attract mating partners over relatively long distances (ROGERS et al. 1996) and might therefore adapt their calls in response to local ambient noise conditions to increase calling range. Calls recorded at DI had a substantially narrower bandwidth compared to the other two study sites. Narrowing the bandwidth of a call and concentrating the acoustic energy of the call in a part of the spectrum with little environmental noise is a strategy in various animal taxa to increase the range of communication in noisy environments (MORTON 1975, RYAN & BRENOWITZ 1985, BERTELLI & TUBARO 2002). Pulse repetition rate also differed between DI



versus AB and DS, which might reflect a similar adaptation to local ambient noise conditions. The fact that signal-to-noise ratio was lowest for recordings originating from DI (Tab. 1) supports this suggestion, unless this proves to correlate with reasons other than higher background noise (i.e., more distant or quieter animals than recorded at the other stations). Several studies have found pulse repetition rate to be the acoustic variable that differs between groups or populations of animals in a wide range of species, although the reason for these differences remains unclear (NEVO et al. 1987, ROTENBERRY et al. 1996, RANKIN & BARLOW 2005).

### Call characteristics transporting phenotypic quality of signaler

The results for HDT duration at all three study sites showed similar distributions for the majority of HDTs. However, at all sites the distribution of the duration of call part 1 was skewed towards a comparatively large proportion of calls having call parts that were longer than the mode. ROGERS (2003) noted that leopard seal vocalizations are potentially energetically very costly calls for the animals to produce and might therefore function to signal fitness to potential mating partners or a competitive response to other vocalizing individuals. In many acoustic species, greater signal energy is typically manifested as greater call intensity, higher repeat rate, or longer call duration (e.g., KLUMP & GERHARDT 1987, WELCH et al. 1998, GREENFIELD 2002). Such signals have in other species been argued to reliably convey information about the signaler's phenotypic or genetic quality because of the energetic costs of increased signal production (RYAN & KEDDY-HECTOR 1992, BRANDT & GREENFIELD 2004, GREENFIELD & RODRIGUEZ 2004). Weddell seals have also been found to lengthen many of their underwater calls in response to overlapping vocalizations of conspecifics, thereby increasing the detectability of their calls and potentially indicating fitness of the calling individual (TERHUNE et al. 1994). In leopard seals, lengthening of broadcast calls, for example of HDT, may serve a similar function, although the number of calls with increased duration might be more restricted by the high energetic costs associated with the production of these calls.

### CONCLUSION

In conclusion, our study has demonstrated that leopard seal HDTs exhibit large-scale similarity across recording locations and that acoustic similarity is not related to geographic distance. Furthermore, our data suggest that a combination of acoustic parameters (i.e., PRR, upper frequency and duration) rather than a single parameter are useful to discriminate leopard seal calls according to recording location. We suggest that differences in local social factors, such as differences in group composition or local abiotic factors might explain these observed differences between recording locations.

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