

Structural variation in the songs of Atlantic walrus breeding in the Canadian High Arctic

Becky Sjare^{1,3}, Ian Stirling^{2,3} and Cheryl Spencer²

¹*Department of Fisheries and Oceans, P.O. Box 5667 St. John's NL, A1C 5X1, Canada*

²*Canadian Wildlife Service, 5320-122 St. Edmonton AB, T6H 3S5, Canada*

³*Biological Sciences, University of Alberta, Edmonton AB, T6G 2E9, Canada*

Abstract

The underwater vocalizations of Atlantic walrus, *Odobenus rosmarus rosmarus*, were recorded during the breeding season at a polynya in the Penny Strait region of the Canadian High Arctic from 1983 to 1989. Mature male walrus emitted two predominant song types, a coda song and a diving vocalization song (DV song). These consisted of a short and long variation of the coda song and a short variation of the DV song that was heard sporadically. The basic structure, organization and temporal characteristics of these song types and variations did not change over the study period. Most males (78%) breeding at the polynya emitted either coda or DV songs 75% of the time that they were engaged in vocal display behaviour. The remainder of the repertoire was comprised of either intermediate songs where the males switched from one song type to the other or aberrant songs that were not recognizable as either song type. In 1988 and 1989, there were significant year-to-year changes in the predominant song type emitted by males in the polynya. It is not certain whether new males moving into the polynya, or perhaps more dominant resident males, influence which song type is emitted during a particular breeding season. Walrus significantly shortened the total duration of their songs and spent more time at the surface when they were attending a herd of females or singing near females as compared to when they sang alone. The duration of singing bouts for some males varied from 8 to at least 65 h and there was a tendency for song type and song duration to vary as the bout progressed. The singing behaviour of male walrus appears to reinforce dominance status in the absence of fighting, suggesting that intra-sexual selection has been important in the evolution of song.

Key words: *Odobenus*, odobenidae, walrus, breeding behaviour, vocalization, vocal behaviour, coda, song types.

Introduction

A considerable amount of pinniped research over the last 20 years has focused on the relationship between the ecological and social factors determining the distribution of receptive females and the subsequent potential for males to acquire multiple mates (e.g., Stirling, 1983; Boness, 1991, 2002; Le Boeuf, 1991). The evolutionary framework that has emerged for pinnipeds from this body of research is responsible for significant advances in understanding of reproductive strategies (Boness, 2002). Boness (2002) noted that this is particularly apparent when the findings on pinnipeds are viewed from within the broader context of existing mating system theory (e.g., Orians, 1969; Jarman, 1974; Bradbury & Vehrencamp 1977; Emlen & Oring, 1977; Clutton-Brock, 1989; Davies, 1991). Few researchers would argue this point. However, it also is important to emphasize that this framework has much to offer in terms of advancing research on the evolution, as well as the structural and functional aspects of marine mammal, and more specifically pinniped, vocal behaviour and communication strategies. As good quality vocal recordings with concurrent behavioural observations become available for a greater number of pinniped species (particularly those mating aquatically), understanding vocal behaviour and communication strategies will parallel and complement what is known about mating strategies and social organization in the future. From this comparative perspective, the walrus is a very interesting ice-breeding pinniped species because there appears to be considerable sub-specific, geographic and habitat-related variation in social organization, mating strategies and vocal behaviour.

Atlantic walrus (*Odobenus rosmarus rosmarus*) breed in pack or land-fast ice habitats in remote Arctic regions during the late winter from February to April (Fay, 1982; Stirling *et al.*, 1983). The species is sexually dimorphic, mates aquatically and

is thought to be moderately polygynous (Stirling, 1983; Boness, 1991). Sjare & Stirling (1996) described the mating system and social organization of a small population of Atlantic walrus breeding at a polynya in land-fast ice as female-defence polygyny. A single large mature male has exclusive access to a herd of walrus for several days at a time and appears to have the opportunity to mate with all females in the herd during his tenure. Pacific walrus (*O. rosmarus divergen*), that breed in pack-ice are thought to exhibit a lek-like mating system where several mature males station themselves in the immediate vicinity of a herd and defend small aquatic territories. On a few occasions, females have been observed to approach, consort, and possibly mate with a particular male (Ray & Watkins, 1975; Fay, 1982; Fay *et al.*, 1984). The inherent gregariousness of female walrus and the degree to which sea ice conditions (pack-ice vs. landfast ice) limit the number and movements of both males and females during the breeding season, appear to be important factors influencing the evolution of social behaviour and the mating system of walrus (Sjare & Stirling, 1996).

During the breeding season when mature males of both subspecies are in the presence of females and other males they produce, loud, repetitive and highly stereotypic underwater vocal displays that have been described as songs (Ray & Watkins, 1975; Stirling *et al.*, 1983, 1987; Fay *et al.*, 1984; Sjare, 1993; Sjare & Stirling, 1996). Most of the song is emitted while the male is completely underwater, but a portion is also given while he floats at the surface with his head submerged in between breaths. A song consists of several long patterned sequences of pulses that vary in length and often are punctuated with ringing bell sounds (Schevill *et al.*, 1966; Ray & Watkins, 1975; Fay, 1982; Stirling *et al.*, 1983, 1987). There are two types of pulsed sounds, the intense, slower repetition rate 'knock' and the less intense, quick 'tap' (Stirling *et al.*, 1983). Knocks have a frequency range of approximately 0.2 to 8.0 kHz with most of the sound energy distributed below 2.0 kHz and a repetition rate of 1–3/s. Taps have a frequency range of approximately 0.2 to 4.0 kHz and a repetition rate of approximately 10/s. Typically, the song of an Atlantic walrus lasts for 3–7 min and is repeated in a bout that may continue for many hours at a time (Stirling *et al.*, 1983, 1987; Sjare, 1993). Although less is known about songs produced by the Pacific walrus, those that have been described were shorter in duration but generally similar in structure and organization (Schevill *et al.*, 1966; Ray & Watkins, 1975; Fay *et al.*, 1984).

There have been two dominant Atlantic walrus song types described, the coda song and the diving vocalization song (Stirling *et al.*, 1983, 1987). These

song types are distinguished from each other based on the pattern of knocks and taps comprising each of the long sequences, and by the presence or absence of specific vocalizations called surface codas, underwater bell-knock codas, and diving vocalizations (Schevill *et al.*, 1966; Ray & Watkins, 1975; Stirling *et al.*, 1983, 1987; Sjare, 1993). These specific vocalizations are short, distinctive series of intense knocks that punctuate either the beginning or end of a long knocking or tapping sequence. In the coda song, certain sequences emitted when the walrus is at the surface end with a surface coda while other underwater sequences end with a bell-knock coda. In the diving vocalization song, there are no surface codas or bell-knock codas; however, there is a distinctive series of loud knocks given just after the walrus dives. This diving vocalization leads into the first long underwater sequence of the song (Stirling *et al.*, 1987). In at least some breeding populations of Atlantic walrus both surface codas and diving vocalizations contain sufficient individual variation to allow reliable identification of mature males (Stirling *et al.*, 1987; Sjare, 1993).

Although walrus of both sexes and all ages are known to emit a wide variety of pulsed grunt and bark-like airborne vocalizations at summer haul-out sites (Miller, 1985), only males are known to sing, and full songs are exclusive to the breeding season. Little is known about the function of walrus songs, but Ray & Watkins (1975) suggested that songs advertised the presence of a male in breeding condition and might be used to establish an underwater territory or dominance hierarchy. In addition to walrus, humpback whales, *Megaptera novaeangliae* (Payne & McVay, 1971) and bowhead whales, *Balaena mysticetus* (Clark & Johnson, 1984) also produce underwater songs during the breeding season. Bearded seals, *Erignathus barbatus* (Ray *et al.*, 1969; Cleator & Stirling, 1989) and Weddell seals, *Leptonchotes weddellii* (Morrice *et al.*, 1994) may also sing during the breeding season.

Prior to this research, knowledge of walrus songs and singing behaviour was based on a limited number of recordings from a few individuals. In addition, earlier studies focused on documenting the stereotypical characteristics of song structure and organization, rather than sources of variation. The objectives of this research were to quantify any seasonal and long-term variability in the structure and organization of coda and diving vocalization songs from a larger sample of males recorded under a diverse range of environmental and social contexts. Emphasis was placed on determining the influence of females and other singing males on the structure and duration of songs. The possible function, behavioural significance, and evolution of walrus songs also are discussed.

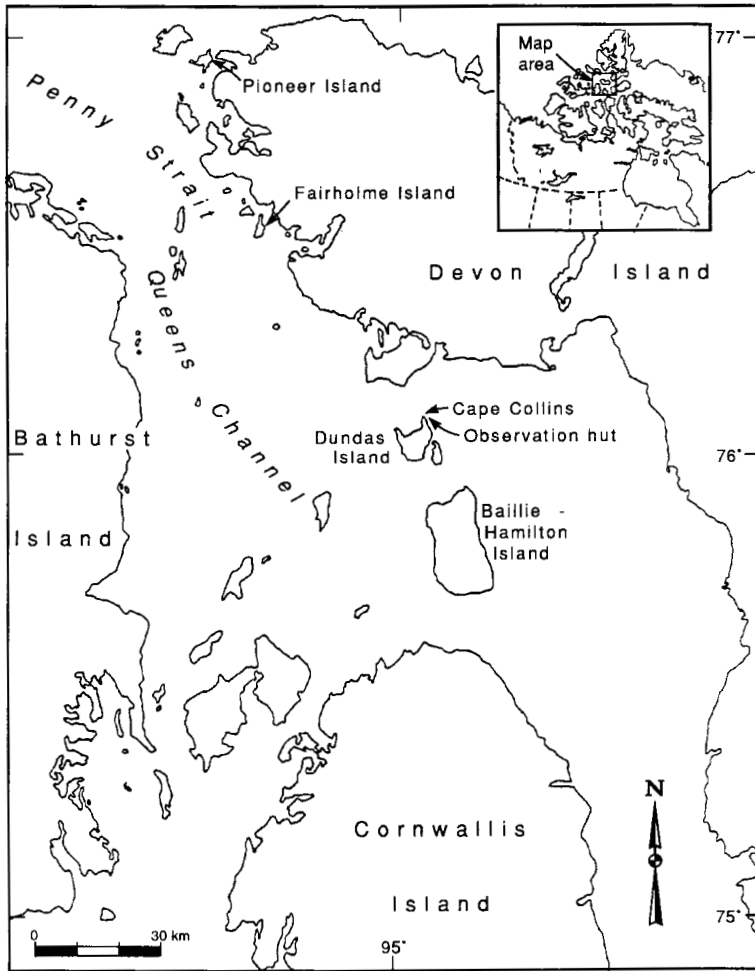


Figure 1. Map of the Dundas Island study area.

Materials and Methods

Study area and recording techniques

Atlantic walruses overwinter and breed at a recurring polynya that forms north of Cape Collins on Dundas Island (76°09'N, 94°52'W) in the Penny Strait region of the central Canadian High Arctic (Kiliaan & Stirling, 1978; Stirling *et al.*, 1981; Fig. 1). Although information on population abundance and stock identity is limited, approximately 200 animals are thought to overwinter in the region with at least 25 to 65 walruses frequenting the polynya in most years (Stirling *et al.*, 1981; Sjare, 1993). The size of the polynya varies seasonally and among years and is a key factor determining the distribution of walruses in the vicinity of Dundas Island. In February and March, it is approximately 0.5 to 2.0 km long and 1.0 to 4.0 km wide, and then by April, it usually quadruples in size as the spring

melt progresses. Walruses use the entire polynya and surrounding land-fast ice area during the breeding season. Other marine mammal species frequenting the study area included bearded seals and ringed seals, *Phoca hispida*.

Behavioural observations and recordings were made from a hut located on an 80-m high cliff overlooking the polynya. Under good sighting and recording conditions it was possible to note the position and movements of walruses up to 5 km away and acoustically monitor the songs of individual males over at least a 10-km radius. Good quality vocal recordings had minimal background noise from wave action, ice or overlapping vocalizations from other walruses or bearded seals. All underwater recordings were made using a Uher 4200 Report Monitor tape recorder and an International Transducer Corporation 6050C

Table 1. Summary of recording information for identified male walruses.

Walrus identification	Date of first and last recording (d/m/y)	Number of days recorded	Number of recording sessions	Hours recorded
8305	13/4/83–18/4/83	2	2	2
8305	11/4/84–24/4/84	5	5	4
8305	4/3/87	1	1	5
8502	16/3/85–24/3/85	3	3	5
8607	9/4/86–27/4/86	3	5	8
8801	27/2/88	1	1	9
8802	2/3/88	1	1	2
8803	18/3/88–19/3/88	2	3	4
8804	19/3/88	1	1	3
8807	27/4/88	1	2	5
BR01	25/4/88	1	1	2
BR04	16/4/88–30/4/88	4	5	9
BR11	28/4/88–29/4/88	2	2	8
BR44	28/4/88	1	1	2
8805	19/3/88–15/4/88	7	10	24
8805	27/3/89–7/4/89	6	13	332
8901	11/2/89	1	1	2
8903	13/2/89–15/4/89	24	44	89
8904	17/2/89–23/3/89	3	3	9
8905	17/2/89–4/4/89	2	2	4
8906	20/2/89–27/2/89	3	4	10
8907	23/2/89–20/3/89	9	26	47
8908	12/2/89–20/4/89	5	9	21
8910	6/3/89–24/3/89	3	6	13
8912	25/2/89–13/4/89	5	6	9
BR02	19/2/89	1	1	6

hydrophone with a built-in pre-amplifier. The frequency response of the recording system was 25 Hz–13 kHz, –12 dB at a tape speed of 4.7 cm/s or 20 Hz–16 kHz, –8.5 dB at a tape speed of 9.5 cm/s. The hydrophone was either submerged through a hole in the ice or suspended from an ice shelf along the southern edge of the polynya to a depth of 3 m. A cable connected the hydrophone to the recording equipment and power sources located in the observation hut. Spectrograms (sampling rate: 20 kHz; frequency range: 0–5 kHz; FFT: 512; bandwidth: 39 Hz) were made using the SIGNAL sound analysis package (Engineering Design, Belmont, Mass.).

Data collection and observational techniques

The underwater songs of individual walruses overwintering and breeding at the Dundas Island polynya were recorded from 1983 through 1989 (Stirling *et al.*, 1987; Sjare, 1993). Prior to 1987, field seasons ran from late March or early April into May. From 1987 to 1989, fieldwork started in early February. The analyses presented here are based on recordings of 23 identifiable males made between 1983 and 1989 (Table 1). Males

recorded before 1988 were selected for analysis if they sang for a long period of time or were recorded on at least three occasions. However, these males were not included in the analysis of year-to-year changes in the occurrence of song types because an earlier study had already examined the available data (Stirling *et al.*, 1987). Two males were recorded in more than 1 year: male 8305 in 1983, 1984, and 1987 and male 8805 in 1988 and 1989.

A total of 3034 songs were selected for detailed analysis from approximately 185 h of good quality recordings. Vocal recordings and concurrent behavioural observations were made using a focal animal approach whenever a singing male moved into the study area. If possible, a focal walrus was recorded continuously for 2.5 h to ensure that a sample size of at least 20 songs was documented. If the singer remained in the study area for longer, additional 1.5-h recording sessions were taped approximately 3 h apart or whenever there was a change in social behaviour. When the male remained in the area for more than 24 h and sufficient recordings were made, the songs were acoustically monitored and transcribed by hand rather than recorded (i.e., a

monitoring session). A singing male could be followed throughout the night and during periods of low light by cueing on individually specific components of the song (Stirling *et al.*, 1987; Sjare, 1993), the intensity of the vocalizations, and the occurrence of accompanying in-air sounds made while the walrus was at the surface. Focal walrus recordings and notes from monitoring sessions were supplemented with a series of shorter duration recordings to document vocal activity on a diel and seasonal basis. These sessions were approximately 30 min long and were recorded every 2 or 3 h on a 24-h basis for 15 days at the beginning, middle, and end of the field season.

An effort was made to obtain multiple recordings and monitoring sessions from known males during different phases of their singing bouts, on different days throughout the breeding season and in varying social contexts. For males with an extensive sample of recordings documenting an entire singing bout, approximately 15 songs were selected randomly from each of the beginning, middle, and end of the bout to determine how songs varied over time. To determine if songs varied seasonally, recordings from the beginning, middle and end of singing bouts taped early in the season, mid-season, and late in the season were selected randomly (when possible) for analysis. The social contexts in which males were recorded often varied considerably, both within a recording session and among days. The most common contexts were: singing alone with no other males visible within 100 m; singing in the presence of a silent male that remained within 50 m; singing when vocal satellite males were near; and singing in the presence of females and calves. During most recordings, it was possible to hear one or more additional males singing at some distance from the focal walrus. Background vocalizations were classified as 'faint' if only a small portion of the song could be heard, 'moderately loud' if portions of an entire song sequence could be recognized and easily followed, or 'loud' if the background vocalizations were almost indistinguishable from those of the focal walrus. To determine how songs varied with changes in these social contexts and the presence of other singers, extensive samples of recordings from some males were sub-sampled randomly for more detailed analyses.

Most male walrus were identified using drawings of tusk characteristics and scar patterns on the neck, shoulders, and back. In addition to these natural marks, nine males were immobilized and branded with two-digit, 12.5-cm high, numbers on their hip and shoulder (Stirling & Sjare, 1988). It was not possible to reliably identify females due to the lack of scarring. Age and sex of walrus were determined using the relative size of the snout and

tusks, muscular development of the upper neck and shoulders, as well as the presence and development of tubercles (Fay, 1982).

Measurement and statistical analysis of walrus songs

A complete walrus song includes both an underwater portion and a surface portion. The surface portion was timed from the moment when the male's head broke the water for the first breath until he dived. The underwater portion was timed from the dive until he surfaced again for the next breath. Therefore, the duration of one full song was considered to be the interval of time between surfacings. All song durations were hand timed (0.01 min) using a stopwatch. Under good observation conditions, it was possible to see the male rise to the surface to breathe and note exactly when his head broke the water for the first breath. Under poor observation conditions, or if the male moved behind an ice floe out of view, his surface and dive times were estimated based on the repetitive and predictable pattern of his vocalizations. The interval between the end of the last underwater knocking sequence and when a male surfaced for his first breath was consistent for an individual. Similarly, the interval between the end of the last knocking sequence emitted at the surface and the onset of a dive also was consistent. Therefore, it was possible to reliably estimate times that could not be observed directly. During a monitoring session, surfacing and dive times were documented along with the transcribed song.

The major song types emitted by walrus breeding at the Dundas Island polynya were reliably distinguished based on the following: (1) the patterning of knocking and tapping sounds that comprised particular sequences, (2) the order in which the sequences were emitted, and (3) the presence or absence of specific vocalizations punctuating the beginning or end of sequences. Specific to the latter feature, coda songs were distinguished from DV songs by the presence or absence of surface codas, underwater bell-knock codas, and diving vocalizations (Stirling *et al.*, 1987). Different variations of each major song type were described based on the repetition or deletion and/or order in which recognizable sequences were emitted. In almost all cases, the terminology used to describe the variations of each song type or any distinctive vocalizations follows Stirling *et al.* (1987). The most notable exception is that the double-knock bell (dkb) sound described in 1987 is now referred to as a double-knock-bell-knock (dk-bk) since there are clearly three pulses with the tonal component associated with the terminal pulse. Bell-like tonal sounds rarely are emitted without at least one preceding pulse.

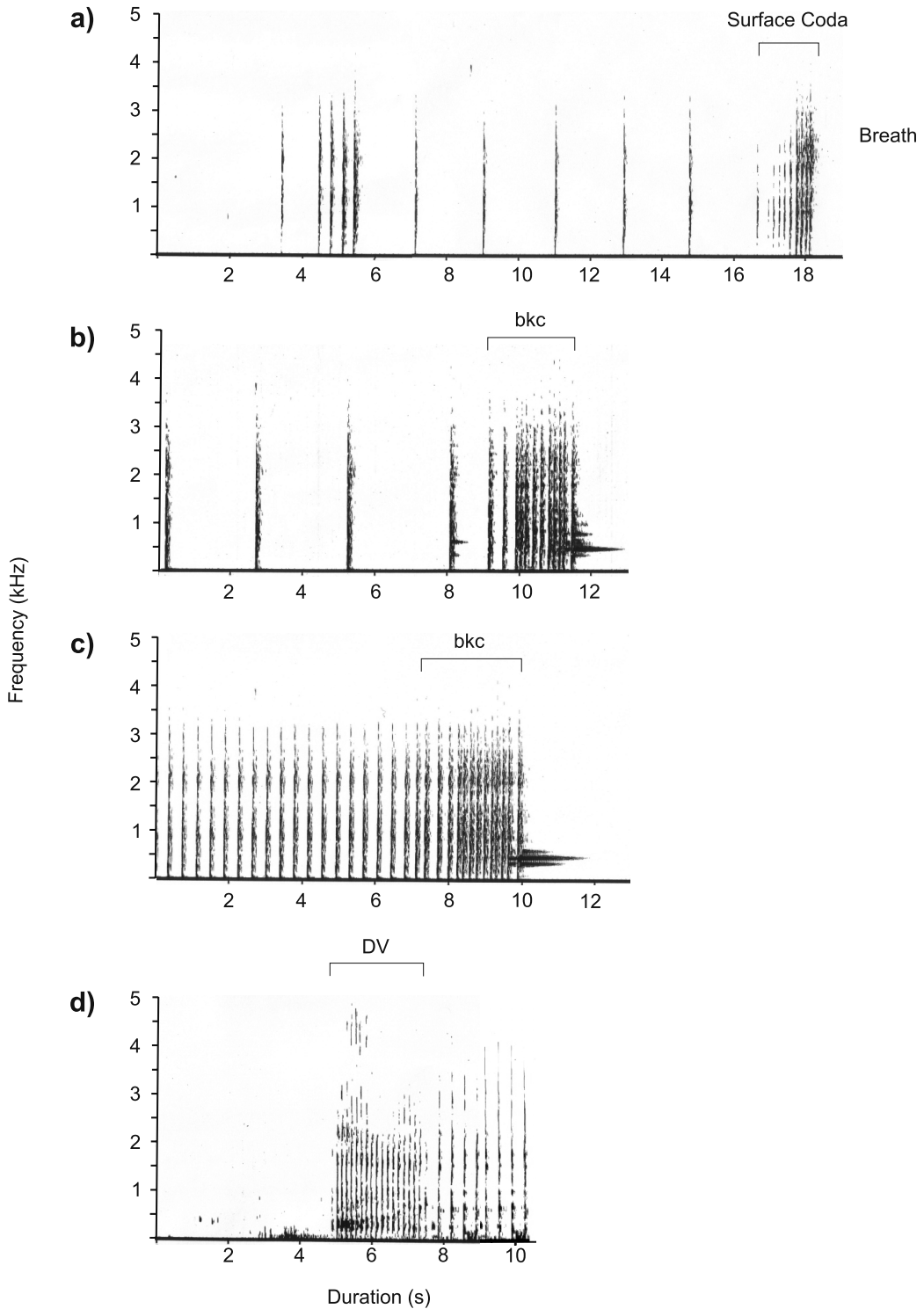


Figure 3. Spectrographs of: a) the k 4k-ts-surface coda sequence of a coda song, b) the bell-knock coda (bkc) terminating the first underwater sequence of the coda song, c) the bkc terminating the third underwater sequence of the coda song, and d) an example of a diving vocalization (DV) at the beginning of the first underwater sequence of the diving vocalization song.

part of the vocal display. In the short coda song, sequence III is consistently omitted. In the long coda song, sequences II and III are repeated so that the order of sequences becomes: I, II, III, II, III, IV (Fig. 2). The structure of an erratic coda song is recognized easily as a coda song, but varies unpredictably in several ways: (1) the cadence of knocking and tapping sounds comprising a sequence may be irregular, (2) sequences may be emitted in a different order, (3) there may be long periods of silence throughout the song, and (4) the singer may take a highly variable number of breaths while the surface.

Diving vocalization songs—Only a few males emitted diving vocalization songs (DV songs) in 1988 or 1989, but a sufficient number of recordings were made to confirm that the overall song structure and organization was similar to that described by Stirling *et al.* (1987). The surface portion is composed of two main sequences and there are no surface codas emitted. The duration of this portion of the song is lengthened or shortened depending on how many k k sequences are emitted and how long the k-ts-2k sequence is (Fig. 2; DV song-sequences labelled 1 and 2 respectively). The underwater portion of the song begins with the distinctive diving vocalization (DV; Fig. 3d) and has six sequences that usually terminate with a bk or a knock-strum (k-strum; Stirling *et al.*, 1983, 1987; Fig. 2). The pattern of knocking and tapping series in each of the long sequences is different from that of the coda song and there are no bell-knock codas (bkc) emitted. It was not possible to confirm with certainty how many consistent and shared variations of this song there may be. However, in addition to the typical DV song, males also sang a short variation where sequences III, IV and V were consistently omitted. Unless stated otherwise, these two variations were combined for analyses. It should be noted that, in addition a DV song, Stirling *et al.* (1987) also described a strum song. However, this song type has not been recorded since 1984 suggesting that it may be an example of an erratic DV song.

Intermediate songs—When males sang underwater they sometimes switched from a coda song to a DV song (or vice versa). On rare occasions, they completed a double switch—coda to DV and then back to coda (or vice versa). Stirling *et al.* (1987) described these vocalizations as intermediate songs (Fig. 2). Their structure and organization often are consistent within an individual, but not shared by all males in the polynya. Switches occur most often during the first half of the underwater portion and usually in the middle of a long knocking or tapping series. However, switches and double switches also

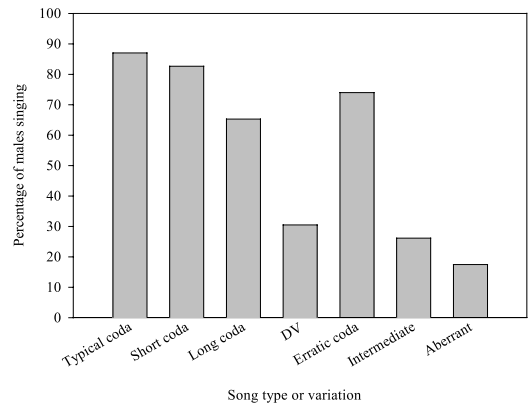


Figure 4. Percentage of males singing each of the song types or variations.

can occur during the surface portion of a song. When the male sings a coda song the switch usually occurs during the tapping series leading up to the surface coda and in the DV song it usually occurs during the tapping series leading up to the 2k (Fig. 2). If a switch occurred in the surface portion of a song it usually carried over into the underwater portion, and the full song was classified as intermediate. Unless stated otherwise all intermediate songs were combined for analysis.

Aberrant songs—In addition to coda, DV, and intermediate songs, males also emit aberrant songs that are characterized by long periods of silence, lack of pattern in the knocking and tapping series composing a sequence, lack of consistency in the order of sequences, noticeably more breaths, and the occurrence of uncharacteristic sounds (e.g., loud grunting or groaning). Most of these unusual song features are observed in both the underwater and surface portion of the display. These songs cannot be recognized as any of the previously described songs types, they usually are not consistent within an individual, and males in the polynya do not share them.

Frequency of occurrence of song types and variations

The percentage of males ($n=23$) that emitted each song type or variation is presented in Figure 4 and the occurrence of each song type or variation as a percentage of an individual male's song repertoire is shown in Figure 5. Of the 20 males that emitted coda song variations, 17 sang them 60–100% of the time; three males (8904, 8907, and 8502) had high proportions of erratic coda songs in their repertoire. Only seven of 23 males emitted DV songs, and of those 8807, BR04, and BR01, sang them almost exclusively while the remaining males sang them

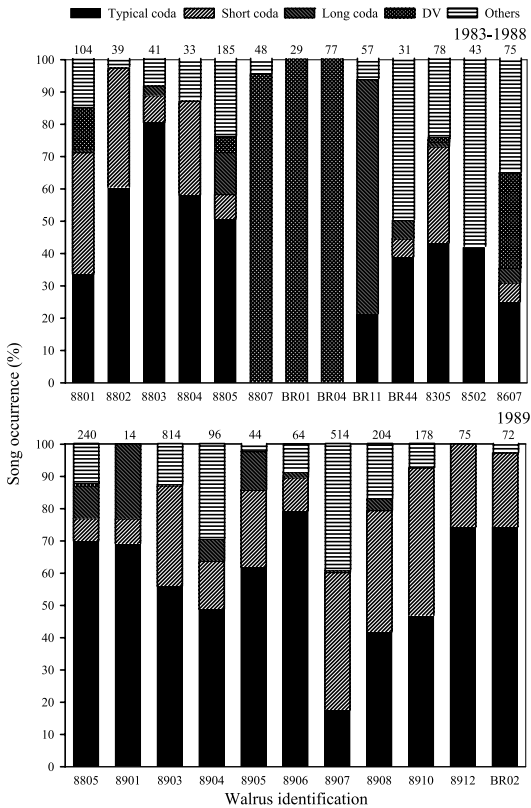


Figure 5. Occurrence of each song type or variation emitted by males in 1983–1988 and in 1989. Category ‘other’ included intermediate, erratic coda songs and aberrant songs. Note that the large sample of songs emitted by male 8805 in 1988 and 89 are shown separately.

<30% of the time. Intermediate songs also were not common with only eight of 23 males singing them. When all song types and variations were categorized as either stereotyped or non-stereotyped, 18 of 23 males sang stereotyped songs at least 75% of the time while 5 males sang them 42–70% of the time (Fig. 5). Stereotyped songs included DV songs and short, typical, and long coda songs. Non-stereotyped songs included erratic coda songs, intermediate songs, and aberrant songs.

There were shifts in the occurrence of certain song types and variations among years (Table 2). A greater proportion of typical coda songs (MWU test, $P < 0.05$, $n = 10, 11$) and fewer DV songs (MWU test, $P < 0.05$, $n = 10, 11$) were emitted in 1989 than in 1988. Only two males, 8305 and 8805, were recorded in more than 1 year. In the case of 8305, sample sizes were small with <30 songs recorded in 2 of the 3 years so songs were combined into all coda songs, intermediate songs and others (aberrant and DV) for analysis. A total of 69%,

Table 2. Between-year differences in the mean frequency of occurrence of songs emitted by walruses recorded in 1988 ($n = 10$ males) and 1989 ($n = 11$ males).

Song type or variation	1988 (%)	1989 (%)
Typical coda	31.7	57.0
Short coda	12.4	22.9
Long coda	8.3	4.5
Erratic coda	3.4	12.0
DV	30.1	<0.1
Intermediate	0.8	<0.1
Aberrant	13.4	3.5

59%, and 82% of the songs emitted were coda songs in 1983, 1984 and 1987, respectively. There were no between-year differences in the proportion of song variations emitted for this male (G-test, $P > 0.10$, $df = 4$, $n = 13, 27, 38$). Male 8805 was recorded extensively in 1988 and 1989 and in both years he sang all song types and variations including short, long and typical codas, intermediate songs and others (aberrant and DV). There were between year differences; he emitted fewer typical coda songs (49% vs. 70%), and more intermediate (21% vs. 8%), and other songs (10% vs. 6%) in 1988 as compared to 1989 (G-test, $P = 0.001$, $df = 4$, $n = 185, 240$).

Variability in song duration

When songs of each male were combined, the mean duration ranged from 3.94–9.34 min (grand mean 6.22, $SD = 1.45$, $n = 23$). When the total duration of the different songs emitted by each male were compared to the male’s typical coda song some basic trends were apparent. Short coda songs were on average 1.43 min ($SD = 0.45$, $n = 19$ males) shorter than typical songs, and long coda songs were 1.40 min ($SD = 0.62$, $n = 10$ males) longer than the typical song. In six of the seven cases when a male emitted both intermediate and typical coda songs, the intermediate songs were on average 0.76 min ($SD = 0.15$, $n = 6$) longer. Diving vocalization songs were 0.57–1.93 min longer than the typical coda songs in the three males that sang them regularly. In seven of 10 cases where males emitted aberrant songs, they were between 1.09 and 7.00 min (mean 2.99, $SD = 2.01$) longer than the typical coda song. In the three remaining cases, they were 1.07–1.83 min shorter than the typical coda song.

When all songs emitted by male 8305 in 1983, 1984 and 1987 were compared across years, no differences were observed in total song duration (KW test, $P > 0.05$ for all comparisons (Table 3). Male 8305 sang an intermediate song in all 3 years, a typical coda song in 1984 and 1987, and a short

Table 3. Between-year differences in the total duration (min) of songs emitted by 8805 and 8305.

Walrus identification	Song type or variation	Year(s)		
		1988	1989	
8805	Total song duration (all songs combined)	7.92 ± 1.50 (171)*	7.55 ± 1.99 (230)	
	Short coda song	6.64 ± 1.03 (13)	5.75 ± 0.97 (15)	
	Typical coda song	7.45 ± 0.98 (86)	7.41 ± 1.20 (164)	
	Long coda song	9.10 ± 0.65 (22)	9.74 ± 1.66 (22)	
	Intermediate song	8.07 ± 1.79 (39)	8.09 ± 2.17 (17)	
8305		1983	1984	1987
	Total song duration (all songs combined)	8.05 ± 1.78 (13)	7.89 ± 1.77 (24)	7.27 ± 1.51 (38)
	Short coda song	7.77 ± 1.01 (7)		6.63 ± 1.65 (13)
	Typical coda song		7.40 ± 1.5 (13)	7.37 ± 1.56 (17)
	Intermediate song	8.02 ± 2.11 (3)	9.14 ± 1.47 (7)	8.28 ± 0.46 (5)

*Mean ± SD (*n*). All songs combined includes erratic coda and aberrant songs.

coda song in 1983 and 1987. There were no among or between-year differences in total duration of these specific songs (KW or MWU test, $P > 0.05$ for all comparisons; Table 3).

When all songs emitted by male 8805 in 1988 and 1989 were compared between years, total song durations were longer in 1988 (MWU test, $P < 0.01$, $n = 171$, 230). Intermediate songs, short, typical, and long coda songs were sung in both years. Short coda songs recorded in 1988 were longer (MWU test, $P < 0.05$, $n = 13$, 15; Table 3), while long coda songs recorded in 1988 were briefer than in 1989 (MWU test, $P < 0.05$, $n = 22$, 22). There were no between-year differences for intermediate songs and typical coda songs.

Breathing patterns and variability in the amount of time spent underwater

The mean number of breaths taken during the surface portion of a song varied from 5.2 to 8.2 (grand mean 6.5, $SD = 0.91$, $n = 23$). The mean time spent at the surface by each male varied from 0.16 to 0.42 min (grand mean 0.27 min, $SD = 0.06$, $n = 23$). For those males singing alone with only faint or moderately loud background vocalizations, the mean number of breaths taken at the surface was positively correlated with the mean time spent underwater (Spearman, $P < 0.005$, $n = 23$). The number of breaths taken at the surface was positively correlated with time spent underwater in 11 of 23 males (Spearman, $P < 0.05$ for all tests).

Factors affecting the frequency of occurrence and the duration of songs

The length of singing bouts—It was not possible to establish a complete seasonal singing profile for

any one male. However, most mature males sang continually for many hours at a time, and in some cases, for 2 or 3 days. Male 8805 was observed in the study area for 27 days in 1988. During that time, he sang for 197 h in eight singing bouts that ranged in duration from 8 to 43 h (mean 23.89, $SD = 10.82$). One bout may have been at least 65 h. Figure 6 summarizes the periods of time he sang and when he was silent. During one silent period, he was observed hauled out along the edge of the polynya approximately 1.0 to 1.5 km from where he had been singing the previous day. Although data on other males are not as complete or free from potentially confounding factors (e.g., changes in social context), long singing bouts were recorded for 11 other walrus (Table 4). Male 8907 may have sung continuously for as long as 81 h; however, it is possible he paused for short periods of time (<2 h) during the nighttime portions of the bout.

There were differences in the frequency of occurrence and in the total duration of songs in four of the singing bouts emitted by male 8805. In all cases, the occurrence of certain songs varied depending on whether it was the beginning, middle, or end of the bout (Table 5). In the first, third, and fourth bouts, the percentage of coda songs decreased as the bout progressed while other songs (i.e., all remaining song types and variations combined) increased. However, in the second bout, the results were opposite. Total song duration increased during the first bout, did not vary in the second or third, and decreased in the fourth. At the beginning of the first bout, mean song duration was $6.89 \text{ min} \pm 0.97$, in the middle it was 7.33 ± 1.46 , and at the end of the bout it was $8.48 \text{ min} \pm 2.08$ (KW test, $P < 0.05$, $n = 20$, 29, 18; the beginning vs. end Tukey pairwise contrast

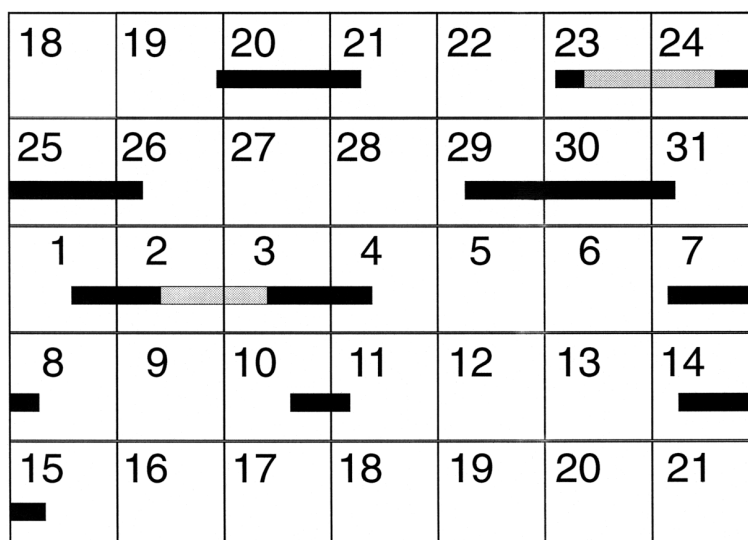


Figure 6. Singing bouts emitted by walrus 8805 during March/April, 1988. Darker shaded lines mark the time periods of continuous singing. Lighter shaded lines indicate time when observations suggest that he was singing, but cannot be confirmed with absolute certainty (these recordings were not included in the calculation of mean song bout duration).

was significant). At the beginning of the fourth bout, mean song duration was 7.72 ± 1.51 , in the middle it was 6.97 ± 1.51 , and at the end of the bout it was 5.10 ± 1.42 (KW test, $P < 0.01$, $n = 25$, 18, 28; the beginning vs. middle Tukey pairwise contrast was not significant but all other contrasts were).

Recording date—Multiple recordings were obtained from six males singing alone with only faint or moderately loud background vocalizations. Two of the males, 8305 and 8805, were recorded in more than 1 year, making it possible to examine the effects of recording date in up to eight different cases, when sample sizes were adequate. The spread between recording dates for each male ranged from 3 to 45 days (mean 18.0; $SD = 13.7$) and all males, except 8305 (in 1983) and 8502, were recorded three times. The occurrence of each song type or variation emitted was influenced by date in five of six cases that could be tested (G -tests; $P < 0.05$ for all comparisons; Table 6). However, except for male 8903, and possibly male 8907, there was little evidence to suggest that songs changed progressively from early to late in the season. Male 8903 was recorded five times. The incidence of short codas decreased slightly over the first three recordings, but then increased sharply for the last two. Male 8907 was recorded three times; the second and third recordings contained much higher proportion of erratic coda songs and fewer short coda songs.

Table 4. Summary of song-bout durations longer than 8 h.

Walrus identification	Date (d/m/y)	Duration of singing bout (h)
8805	27/3/89	8
	31/3/89	8
8907	6–7/4/89	41
	23–26/2/89	57
	11/3/89	11
	17–20/3/89	81
8908	11/4/89	14
	17/4/89	8
	20/4/89	13
8910	24/4/89	8
8912	7/3/89	12
8903	13/3/89	10
	14/3/89	10
	25–26/3/89	33
	5/4/89	21
8801	27/2/88	10
8807	27/4/88	8
BR04	16–17/4/88	16
BR11	28–29/4/88	18
8502	16/3/85	14
	19/3/85	15
	20/3/85	21
	24/3/85	17
8607	27/4/86	13

Table 5. The relationship between song frequency of occurrence and location in song-bout (male 8805 in 1988 and 1989).

Date	Song type or variation	Location in bout			G-test statistic
		Beginning	Middle	End	
19–21 March 88	Short coda	1–7 h 40.0 (8/20)	8–15 h 24.1 (7/29)	16–31 h 0	G=13.272 P=0.010
	Typical coda	25.0 (5/20)	44.8 (13/29)	50.0 (9/18)	
	Other*	35.0 (7/20)	31.1 (9/29)	50.0 (9/18)	
1–2 April 88	All coda songs**	1–3 h 20.0 (4/20)		9–16 h 77 (10/13)	G=10.926 P=0.001
	Other	80.0 (16/20)		23.0 (3/13)	
14–15 April 88	Typical coda	1–3 h 57.9 (11/19)	8–14 h 85.7 (18/21)	20–24 h 31.3 (5/16)	G=15.443 P=0.004
	Long coda	31.6 (6/19)	14.3 (3/21)	37.5 (6/16)	
	Other	10.5 (2/19)	0	31.2 (5/16)	
6–7 April 89	All coda songs	1–7 h 100.00 (25/25)	17–19 h 88.9 (16/18)	37–41 h 64.3 (18/28)	G=21.241 P=0.001
	Other	0	11.1 (21/18)	35.7 (10/28)	

*Other=intermediate, DV, erratic coda and aberrant songs combined.

**All coda songs=short, typical and long coda songs combined.

The total duration of each male's songs varied with date in two of eight cases. Male 8903 progressively shortened his songs throughout the season from a mean of 9.01 min \pm 2.90 to 6.64 \pm 0.93 by 24 March, and to 6.00 min \pm 1.35 by the end of the season (KW test, $P < 0.001$, $n = 15, 19, 12, 14, 26$). Pairwise contrasts between the first recording and those done on 8 and 15 of April were significant as was the contrast between the 27 February recording and the 8 April session (Tukey tests, $P < 0.05$; Table 6 for reference). Male 8805 (recorded in 1988) emitted his longest songs in mid-season and the only significant pairwise contrast was between the 19 March and 1 April recording sessions (KW test $P < 0.001$, $n = 63, 41, 67$; Tukey tests $P < 0.05$). During the first recording session mean song duration was 7.52 min \pm 1.62 and by early April it was 8.55 min \pm 1.45. Songs of 8805 (recorded in 1989) did not vary with date. Although male 8907 was recorded over a 25-day period, and there was a significant shift in proportion of song types over that period, the total durations of his songs did not vary.

Age and dominance status—To evaluate the importance of relative age and dominance status on singing behaviour, males were divided into three groups: mature males >15 years of age that were known to have attended a herd of females (attending males); mature males >15 years of

age that were never observed to attend a herd of females (mature males); and males 10–15 years of age that were never observed to attend a herd of females (young adult males). Unfortunately, small sample sizes hampered analyses and interpretation.

Attending males recorded in 1988 sang exclusively DV songs while young adult males and mature males predominantly sang coda song variations (54% and 78%, respectively). A comparison between the proportion of DV songs and the proportion of all 'other' song types and variations combined by male, showed this difference was significant (MWU test, $P < 0.05$, $n = 2$ males, 8 males). However, despite this strong split in song types, 2 of the 4 young adult males emitted a significant proportion of DV songs (95% and 13%) compared to only 5% emitted by one of the mature males. In 1989, attending males and young adult males sang a greater number of short coda songs compared with mature males (KW test, $P = 0.01$; Tukey test, $P < 0.05$ $n = 4, 3, 4$; Table 7). In this respect, song repertoires of young adult males were more similar to the attending males than to other mature males in 1989.

Given that in 1988 attending males emitted exclusively DV songs while all other males emitted mainly coda songs, it was not possible to separate an age or dominance status effect from a possible song-type effect on temporal song characteristics.

Table 6. The relationship between the frequency of occurrence of songs and recording date. All walruses were recorded singing alone. Each cell entry shows recording date, sample size and percent of each song type/variation in sample.

Walrus identification	Song type or variation	Date (d/m/y) and number of recordings sessions obtained				
		Recording I	Recording II	Recording III	Recording IV	Recording V
8903	Short coda	18/2/89 <i>n</i> =15 16.7	27/2/89 <i>n</i> =20 10.0	24/3/89 <i>n</i> =12 0	8/4/89 <i>n</i> =16 56.3	15/4/89 <i>n</i> =26 48.0
	Typical coda	83.3	90.0	100.0	43.7	52.0
8907	Short coda	24/2/89 <i>n</i> =71 56.3	11/3/89 <i>n</i> =39 30.8	19/3/89 <i>n</i> =43 16.3		
	Typical coda	23.9	2.6	20.9		
	Erratic coda	19.7	66.7	62.8		
8805	Short coda	19/3/88 <i>n</i> =71 21.1	1/4/88 <i>n</i> =44 11.4	14/4/88 <i>n</i> =70 24.3		
	Typical coda	40.9	40.9	61.4		
	Intermediate	26.8	29.6	10.0		
	Aberrant	11.3	18.2	4.3		
8607	All coda songs	9/4/86 <i>n</i> =13 0	24/4/86 <i>n</i> =18 61.1	27/4/86 <i>n</i> =44 29.6		
	DV Song	38.5	0	34.0		
	Other	61.5	38.9	36.4		
8502	Short coda	16/3/85 <i>n</i> =38 0	19/3/85 <i>n</i> =36 11.1			
	Typical coda	42.1	38.9			
	Erratic coda	57.9	50.0			

Table 7. The relationship between relative age/social status and the mean frequency of occurrence of songs emitted by walruses in 1989.

Song type or variation	Attending male (%) <i>n</i> =4	Mature male (%) <i>n</i> =3	Young adult male (%) <i>n</i> =4
Short coda	29.9	8.7	25.7
Typical coda	48.0	75.2	56.8
Long coda	0.4	8.6	5.6
Erratic coda	21.3	3.0	9.2
Intermediate	0	0.1	0
Other (dv, aberrant)	0.4	4.3	2.7

To further confound the analysis, one of the attending males was only recorded while singing near females (see comments below). Mean song duration varied little from a low 6.38 min \pm 1.36 for mature males to a high of 6.77 min \pm 1.35 for young adult males. In 1989, the mean song duration was

5.37 min \pm 1.02 for attending males, 7.90 min \pm 1.30 for mature males, and 5.23 min \pm 1.44 for young adult males; these differences were not significant (KW test, $0.05 < P < 0.10$, $n=4, 3, 4$). However, mature males did take more breaths at the surface (7.8 ± 0.22) than either attending males (5.9 ± 0.58) or young adult males (5.7 ± 0.60 ; KW test, $P < 0.050$, Tukey test, $P < 0.05$, $n=4, 3, 4$).

Social context—Most males in this study were recorded while singing alone, but five were recorded during other circumstances (Tables 8 and 9). Male 8903 sang alone, when a silent male was nearby, when other mature males were singing intermittently within 100 m of him, and when he was attending a herd of females. Males 8907 and 8910 were recorded singing under similar conditions, though neither of them was accompanied by a silent male on a regularly basis. Instead, the analysis included songs recorded when these males were within 100 m of a small herd of females and calves, but were not interacting with them directly (i.e.,

Table 8. Relationship between social context and total song duration (min), number of breaths at surface and proportion of time at the surface.

Walrus identification	Song variable	Singing alone; background songs faint-moderate	Singing alone; background songs loud	Singing alone; background songs loud and satellite male nearby	Singing alone; background songs moderate and females in area but not interacting with singing male	Attending male
8903	Mean song duration ± SD (<i>n</i>)	6.87 ± 1.88 (96) a**	7.01 ± 1.71 (61) b	6.37 ± 1.49 (137)		6.05 ± 1.90 (189) ab
	Mean no. breaths ± SD (<i>n</i>)	5.8 ± 1.2 (99) b	6.0 ± 1.02 (66)	6.0 ± 1.18 (148) a		7.0 ± 1.51 (189) ab
	Mean % time at surface	22.9% (96) a	24.8% (61)	26.4% (137) b		29.1% (189) ab
8910		5.16 ± 0.88 (37) abc		4.36 ± 1.11 (31) ade		3.64 ± 0.78 (53) ce
		5.3 ± 0.76 (38)		5.1 ± 1.30 (32)	3.64 ± 0.78 (17) bd	5.4 ± 1.08 (36)
		26.4% (37)		26.5% (31)	24.4% (17)	26.9% (53)
8907		6.85 ± 1.73 (108) abc		5.97 ± 2.03 (181) ade		3.71 ± 1.56 (97) ce
		6.0 ± 1.22 (115)		5.5 ± 1.15 (186)	3.95 ± 1.25 (37) bd	5.8 ± 2.15 (102)
		15.1% (108) abc		17.6% (181) ade	6.2 ± 2.41 (37)	26.5% (97) ce
BR02		4.43 ± 0.76 (47) a				3.49 ± 0.86 (16) a
		6.6 ± 0.88 (46)				6.5 ± 1.41 (15)
		28.2% (47)				31.8% (16)
BR04		(drugged male nearby)		(near herd of immature males)		5.44 ± 1.16 (25) ab
		10.52 ± 2.6 (7) a		8.10 ± 1.60 (11) b		6.7 ± 1.35 (27)
		7.4 ± 2.6 (9)		7.5 ± 2.03 (13)		21.8% (25) ab
	16.1% (7)		15.1% (11) b			

**Matching letters indicate significant multiple-pairwise comparisons within an individual and across social contexts.

Table 9. The relationship between social context and the frequency of occurrence of each song type or variation in 1989.

Walrus identification	Song variation	Singing alone; background songs moderate	Singing alone; background songs loud	Singing alone; background songs loud; satellite male nearby	Singing alone; background songs moderate; females nearby but not interacting with singer	Attending male
8903	Short coda	26.5 (26/98)	18.5 (12/65)	36.2 (51/141)		38.5 (75/195)
	Typical coda	68.4 (67/98)	69.2 (45/65)	56.0 (79/141)		45.3 (88/195)
	Erratic coda	5.1 (5/98)	12.3 (8/65)	7.8 (11/141)		16.4 (32/195)
8910	"	2.8 (1/36)		37.5 (12/32)	47.1 (8/17)	81.4 (35/43)
		75.0 (27/36)		43.7 (14/32)	52.9 (9/17)	18.6 (8/43)
		22.2 (8/36)		18.8 (6/32)	0	0
8907	"	47.3 (52/110)		29.5 (56/190)	42.9 (18/42)	61.9 (65/105)
		14.5 (16/110)		21.1 (40/190)	14.3 (6/42)	5.7 (6/105)
		38.2 (42/110)		49.4 (94/190)	42.9 (18/42)	31.4 (34/105)
BR02	"	13.0 (6/46)				62.5 (10/16)
		87.0 (40/46)				25.0 (4/16)
		0				12.5 (2/16)
BR04	(near drugged male)					
	Full DV song	77.8 (7/9)		35.7 (5/14)		3.6 (1/28)
	Short DV song	22.2 (2/9)		64.3 (9/14)		96.4 (27/28)

they were not attending males). Male BR02 was recorded alone and when he sang and briefly interacted with a female and her calf. Male BR04 was recorded while singing alone at a hole in the ice beside a mature male that had been drugged and was being fitted with a VHF radio tag. He also sang alone at a hole directly in front of a herd of young adult males, as well as when he attended a herd of females (in all cases background songs were faint to moderately loud).

All five males sang their longest songs when they were alone and their shortest songs when there were females in the immediate area (KW tests, $P < 0.001$; Tukey tests, $P < 0.05$, for each male; Table 8). Three of the five males spent a larger portion of time at the surface when they were singing near females compared to when they sang alone or when other males were in the area (KW tests, $P < 0.003$; Tukey tests, $P < 0.05$, for each male). Four of the males emitted short, typical and erratic coda songs and each significantly varied the frequency of occurrence of these songs in relation to social context. For those males that predominantly sang coda songs, a greater number of short and erratic coda songs, and fewer typical coda songs, were emitted when males were in the vicinity of females (G-tests, $P < 0.05$ for all comparisons Table 9). Male BR04 emitted DV songs, and although it is not certain that a consistent short version of this song exists, he sang the full song when alone and a consistent short variation (sequences III, IV and V were omitted) when he was attending the herd of females (G-test, $P < 0.05$; Table 9).

Discussion

Variability in the structure and organization of walrus songs

Underwater recordings of 23 mature male Atlantic walruses, made in a number of different social contexts, confirm that walrus songs generally are consistent within and among individuals frequenting a polynya (Ray & Watkins, 1975; Stirling *et al.*, 1983, 1987). Eighteen out of 23 males sang coda song variations or DV songs at least 75% of the time. The basic structure and total duration of a typical coda and DV song has not changed from 1983–1989 (Stirling *et al.*, 1983, 1987; this study). Although the numbers of recordings from identified male walruses have been increased in this study, there are still problems with small, non-random samples obtained from a limited number of individuals in one geographic location. This is a problem common to many marine mammal vocalization studies, and in the case of walruses, it will only be addressed as more dedicated research projects are undertaken in other Arctic areas in the future.

Earlier research on walrus vocal behaviour focused on the surprisingly consistent nature of songs and did not address variation within these patterns. However, Stirling *et al.* (1987) noted that shorter and longer coda songs, and shorter DV songs sometimes occurred, but did not describe them as song variations. In addition to DV songs, typical, short, and long coda songs, males also emit an erratic coda song, an intermediate song, and an aberrant song. These differ from the previously mentioned DV and coda songs in that they often are not individually consistent and all males frequenting the Dundas Island polynya do not share the structure and organization of each song. This is particularly true for the aberrant songs. Given the larger sample of males and songs in the sample, this variability is not surprising and does not seriously alter the conclusions of earlier studies that emphasized consistency. However, these data show that less consistent songs are also a component of some males' song repertoire.

Because this species breeds and sings during the winter in remote Arctic areas, opportunities to record walrus songs in the wild are limited, and few recordings are available for comparative purposes. Ray & Watkins (1975) observed and recorded a male Pacific walrus for 5 h during March in the Bering Sea. Based on the information presented, the composition and order of the underwater sequences emitted by this male differed from any of the songs described here. However, the overall song structure resembled the short coda song; both surface and underwater bell-knock-codas were recorded. The total duration of 15 songs emitted by the male averaged 2.40 min long, which is significantly shorter than any of the songs recorded at the Dundas Island polynya. In another isolated observation, the surface/dive times for three male Pacific walruses displaying near a herd of females indicated that their songs were also approximately 3 min long (no recordings were made; Fay *et al.*, 1984). The possible significance of these short duration songs is discussed in more detail later.

The only other marine mammal species that has a vocal display similar to the walrus, is the humpback whale (Payne & McVay, 1971; Payne *et al.*, 1983). Compared to walrus songs, whale songs have longer durations and are composed of a greater variety of sounds. Nevertheless, there are some interesting organizational similarities. In humpback whale songs, individual sounds are called units; several units are combined into a sub-phrase; two or more sub-phrases are combined in a particular order into a phrase; repeated phrases sung in a particular order comprise a theme; and several themes are sung in a particular order to make up a song (Payne & McVay, 1971; Payne *et al.*, 1983). In walrus songs, the individual knocks and taps are

emitted in series; several series are combined in a specific order to form a sequence; and, specific sequences are emitted in a particular order to make up a song. However, an interesting difference is that, in the case of humpback whales, all males in a region sing the same song and the structure of many of the units and phrases progressively change over time suggesting that there is a cultural transmission or learning process occurring (Winn & Winn, 1978; Payne *et al.*, 1983; Noad *et al.*, 2000). Walrus breeding at the Dundas Island polynya switch between song types within a season and can exhibit abrupt shifts in song usage between years, yet the basic structure and organization of the songs has not changed since 1983. Presently it is not known whether this perception of stability is in part due to the lack of comparative recordings from walrus populations in other geographic areas.

The consistent structure and organization of humpback whales songs may facilitate learning of the complex vocal display. Payne (1991) suggested that phrases and themes that are repeated at certain points in the song might help 'remind' the whale of what comes next. Although there was no quantitative evidence of this type of progressive learning by successful breeding male walrus, erratic coda songs were recognized based on the presence of surface codas and bell-knock-codas in the appropriate location in the song. It appeared that even when walrus sang erratically they would hone in on the terminal portion of a sequence and produce a quality rendition of that portion of the song (Stirling & Sjare, unpublished data). Juvenile males <10 years of age often emitted long, erratic sequences of knocking and tapping series that were not recognizable as a full song. However, depending on the age of the animal, some of these erratic sequences ended with the appropriate bell-knock-coda. The older the walrus, the better the rendition of the song became (Sjare & Stirling, unpublished data).

Factors influencing the frequency of occurrence and duration of walrus songs

A male's relative age and social status, social context, duration of singing bouts, and date of recording date all appear to influence the frequency of occurrence of songs and song duration. The most important factor appeared to be the presence of females near the singer. Males that were recorded in several different social contexts significantly shortened the total duration of their songs, emitted relatively more short coda songs, and spent more time at the surface when they were attending males or were singing near females, compared to when they sang alone.

There are at least two reasons why males might vary their songs while attending a herd or while

singing near females. Silent, young adult males associating with the herd often approach female herd members as soon as the attending male dives underwater to sing the underwater portion of his song. Occasionally, these younger males have time to initiate courtship behaviour and, on rare occasions a partial mount (Sjare & Stirling, 1996). Just before the attending male surfaces, the young adult male moves several meters away from the female. The attending male may shorten his song and spend more time at the surface, to minimize the possibility of interactions between younger males and females. Shortening the song also means that the number of full songs emitted per hour would increase, and that surface codas and DV vocalizations would be heard more often. Given that surface codas (Stirling *et al.*, 1987; Sjare, 1993), and possibly diving vocalizations (Stirling *et al.*, 1987), convey information on the identity of a male, short songs may allow an attending male to reinforce or advertise his identity. These two factors may also explain why the songs of Pacific walrus are so brief. The much higher densities of males in the immediate vicinity of large herds of females in the breeding areas may result in a higher incidence of male-male aggressive interactions and intensify the need for short songs (Sjare & Stirling, 1996).

The relationship of relative age and social status to the proportion of song types and variations emitted and to song duration could not be confirmed due to small sample sizes. However, in 1989, there appeared to be more similarities in the frequency of occurrence and total song duration between the songs of young adult males and attending males than there were between mature males and attending males. The reasons for this are not clear. However, if a mature walrus greater than approximately 15 years of age has not established himself as a successful breeding male, there may be less incentive for him to sing in a particular way. At least some of the young adult males still have an opportunity to become dominant and the pressure of this competition may be reflected in their singing behaviour.

It was difficult to identify seasonal trends in the frequency of occurrence of songs or song duration because few males were recorded more than once in comparable social contexts. Male 8903 sang relatively few short coda songs for most of the season, then sharply increased the number near its end; male 8907 emitted a high proportion of erratic coda songs during the last half of the season. For male 8903, it is questionable whether the trend was seasonal or related to more interactions with females. As the season progressed, this male spent more time attending females and singing short coda songs. By the end of the season, this shift in song variation may have carried over to times when he

was singing alone. Based on available data, male 8907 did not spend more time with females as the season progressed, so the increase in erratic coda songs late in the season may reflect a seasonal trend for this male. However, it appears that seasonal effects may be minor and perhaps masked by other factors. There is little evidence of a seasonal trend in song duration. Only two of eight males varied song duration with recording date; male 8903 progressively shortened his songs throughout the season while 8805 (recorded in 1989) sang his longest songs at mid-season. Results for 8903 are consistent with what would be expected given that short coda songs are shorter than typical coda songs. It is difficult to interpret the results for 8805; there was no obvious explanation for the long song during the mid-season recording.

There were several between-year shifts in the proportions of song types and variations emitted. A greater number of typical coda songs and fewer DV songs were recorded in 1989 compared with 1988. Stirling *et al.* (1987) also documented a strong difference in proportions of coda and DV songs emitted in 1983 as compared to 1984. Although results of the two studies are not directly comparable because the earlier study included strum songs, and did not categorize coda songs into short, typical, and long variations, it appears that year-to-year changes in proportions of song types and variations occur regularly. However, it is not apparent why.

One possibility is that shifts occur when new males move into the polynya. For this explanation to be plausible, individual males would have to show a strong and consistent preference for a particular song type or variation. Existing data indicate that this is not always true. Many, if not all, mature males frequenting the polynya can sing all major song types and variations (Stirling *et al.*, 1987; this study). In addition, some males change the proportions of song types and variations significantly between years. Male 8805 sang more typical coda songs and fewer DV songs in 1989, compared with 1988. More importantly, this shift generally reflected what other males in the polynya were singing, which suggests that males imitate one another. Perhaps if the most dominant males in the polynya are singing coda songs, other males may do so. There is some support for this idea; in 1989, the four attending males all sang variations of the coda song and so did all other males (virtually no DV songs were recorded in that year). In 1988, the two attending males emitted exclusively DV songs, and three of the remaining eight males sang DV songs exclusively or part of the time. There is extensive evidence for song learning, song matching and mimicry in birds (e.g., Falls, 1982). Almost all oscine bird species that sing complex songs or have

song repertoires learn them from other individuals. In most cases, the 'tutor' is the father or another male that the young bird interacts with (Falls, 1982; Kroodsma, 1982). For example, village indigo birds (*Vidua chalybeata*), are polygynous and young males are known to copy the songs of successful breeding males (Payne & Payne, 1977; Payne, 1985). In the case of walrus, juvenile males were regularly observed to silently 'shadow' an attending male's dive pattern while he was singing (Sjare & Stirling, 1996).

The length of a mature male walrus's singing bout is one of the longest, if not the longest, ever documented for a mammal. These bouts are emitted on a regular basis for at least 2 months of the breeding season. The proportion of song types, song variations, and song duration vary depending on whether they were emitted near the beginning, middle or end of a singing bout. Male 8805 sang fewer coda songs and a greater number of intermediate and aberrant songs as the bout progressed. Results for changes in song duration were difficult to interpret because of the small sample sizes. However, durations varied in two of four cases; on one occasion, male 8805 gradually lengthened his songs and on the other he shortened them. Given the length of the singing bouts one might expect that fatigue or monotony could influence the occurrence of song types and variations and the duration of songs. Either of these factors would generate higher variation near the end of a singing bout. Data presented here support this prediction. In birds, it has been suggested that one function for a large repertoire of songs is to enhance the effectiveness of the display by decreasing monotony (Hartshorne, 1956, 1973; Kroodsma, 1978).

The function and evolution of walrus songs

Little is known about the function of walrus songs or the selective pressures that have shaped them. Ray & Watkins (1975) suggested that songs advertised the presence of a male in breeding condition and also may be used to establish an underwater territory or dominance hierarchy. Observations on walrus breeding and singing behaviour in this study suggest that a male's singing ability helps to maintain his dominance status without engaging in physical interactions, and that intra-sexual selection has been important in song evolution (Sjare & Stirling, 1996). Males that sang most extensively were the ones that gained access to herds of females and calves. Young adult males in the immediate vicinity of a herd of females curtailed their singing activities in the presence of an attending male. All males had the opportunity to assess each other's singing capabilities for long periods because of the

restricted access to open water and the stability of the sea ice in the area. Limited observations suggest that males respond to singing of other males (Sjare, 1993; Sjare & Stirling, 1996). To date, there are insufficient data to determine whether certain aspects of a male's singing ability are related to body condition, fighting ability or some other aspect of reproductive success. Observations of aggressive interactions involving physical contact between males were rare during the study. Without such data it is not possible to confirm with certainty the role of singing behaviour in the maintenance of dominance relationships, but it does appear to be important.

There is less evidence to support the idea that male Atlantic walruses use their songs to establish an acoustic territory. The movements of female herds and attending males were wide-ranging and variable depending on tide, currents, water-surface conditions, and ice conditions. Even when no females were visible, singing males moved about the polynya and did not appear to defend a specific area. There also was no evidence that songs functioned to attract individual females or groups of females to the location of a singer. However, it was difficult to reliably identify female walruses, so tracking their movements relative to singing males was significantly hampered.

Even though there is little evidence to confirm that Atlantic walrus songs function to attract females, female preferences could be important. If some aspect of singing ability conveys information about a male's social status, females, like males, have ample opportunity to monitor and assess the songs of all males during the breeding season. They also have an opportunity to acquire information on the dominance status of each singer. In addition, lone females are probably capable of recognizing which males spend the most time attending herds, based on the song types and variations being emitted (i.e., males sing a higher proportion of short coda and DV songs when attending a herd). Given this scenario, it is probably too simplistic to conclude that the function of walrus songs have been shaped only by intra-sexual selection. Tyack (1981; 1999) suggested that humpback whale songs also evolved in response to both intra- and inter-selection pressures. However, more recent observations on interactions of singing whales with other males support the hypothesis that song may function in male social ordering and that intra-selection is more important (Darling & Berube, 2001). Numerous studies of bird songs also have demonstrated that some species emit song types that have relatively distinctive, but not necessarily mutually, exclusive intra- and inter-sexual functions (e.g. Baptista, 1978; Payne, 1979; Catchpole, 1987; Kroodsma *et al.*, 1987).

If males use singing behaviour to assess their opponents' social status and potential fighting ability, or if females use singing to assess a male's fitness, then the assessment criteria must be closely linked to those traits (Maynard Smith & Price, 1973; Parker, 1974; Zahavi, 1975; Maynard Smith & Parker, 1976; Zahavi, 1977). In many species, the vocal displays of males during the breeding season appear to be strenuous and energetically expensive (e.g., Clutton-Brock & Albon, 1979; Taigen & Wells, 1985; Wells & Taigen, 1986; Robertson, 1986). There are also a number of acoustic features in a vocal display that could serve as 'copy proof' criteria of a male's general body condition or size, for example, the fundamental frequency of the call in some species of birds and frogs (Davis & Halliday, 1978; Morton, 1977). To fully understand the function of walrus songs it will be necessary to identify which song attributes males and females respond to.

One such attribute may be how long a male sings. Humpback whales sing complex songs that are repeated every 5 to 30 min, in bouts that can last for as long as 22 h (Winn & Winn, 1978). Walruses emitted songs that were repeated approximately every 6.5 min, in bouts that commonly lasted 48 h. There was good evidence that some males sang continuously for at least 65 h, and possibly, for as long as 81 h in one case. Although the duration of virtually all the individual dives made during a singing bout were well within the estimated aerobic dive limit for walruses (Nowicki *et al.*, 1997), the length of time over which males can sustain continuous singing may be both an accurate and reliable indicator of general condition. Both male and female walruses have the opportunity to assess this feature of singing behaviour. Attending males spent a longer time in the polynya and sang for longer periods of time than other males (Sjare, 1993; Sjare & Stirling, 1996). At the end of the breeding season in May, some of the largest and oldest males were noticeably emaciated. In most cases it was not possible to confirm if they were the same individuals that sang extensively during the peak of the breeding season, but it is likely that they were (most scars used to identify males in the water are not visible when the male is hauled out). These observations suggest that a male's ability to sing continuously for long periods of time during the entire breeding season may be linked to body condition, particularly blubber reserves. Thus, the duration of a male's singing bout and the amount of recovery, or rest time between bouts may convey information about his general physical condition. Positive relationships among body condition, breeding performance and reproductive success have been documented for several species of land breeding pinnipeds (e.g. Le Boeuf, 1972; Le Boeuf

& Reiter, 1988; Deutsch *et al.*, 1990; Boness, 1991; Wells *et al.*, 1999).

Additional supporting evidence linking a male's ability to sing for long periods of time with physical condition relates to the striking similarity between the dive pattern of a feeding walrus and the dive pattern of a singing walrus during the breeding season. Feeding walruses dive for approximately 5 min and then remain at the surface for 1–2 min (Fay, 1982). Data obtained by satellite telemetry showed that Atlantic walruses feeding in Greenland waters dive continuously for an average of 17.33 h/day for 2–4 days at a time. At the end of the feeding bout they return to a land or ice haul-out site to rest for approximately 2 days (Born & Knutsen, 1990). Numerous researchers have demonstrated that elaborate communication signals can evolve from common behaviours that gradually become ritualized (e.g., Tinbergen, 1959; Alcock, 1989). For example, the courtship and mating displays of a variety of bird and insect species involve ritualized aspects of feeding behaviour (e.g. Kessel, 1955; Lindauer, 1961; E.O. Wilson, 1971). Further studies addressing similarities between walrus foraging behaviour and singing behaviour during the breeding season may provide a better understanding of the function and evolution of song in this species.

Acknowledgments

We thank Dennis Andriashek and Wendy Calvert for helping with all aspects of the field and laboratory work; their contributions were essential for the success of the project. Constructive comments on earlier drafts of the manuscript were received from Jan Murie, John Holmes, Linda Fedigan and Ted Miller. We also thank David Keith, Eric Born, Peter Achuff and Ed Struzik for their assistance in the field. Logistic support was provided by the Polar Continental Shelf Project; we particularly thank Jim Godden and Barry Hough for their help. Financial support was obtained from the following agencies and organizations: World Wildlife Fund (Canada), Polar Continental Shelf Project, Canadian Wildlife Service, Department of Fisheries and Oceans Subvention Program, University of Alberta, Arctic Institute of North America and the Alberta Government Scholarship Program.

Literature Cited

- Alcock, J. (1989) *Animal Behavior: An Evolutionary Approach*. Sinauer Associates, Inc. Sunderland, Mass.
- Baptista, L. F. (1978) Territorial, courtship and duet songs of the Cuban Grassquit (*Tiaris canora*). *Journal für Ornithologie* **119**, 91–101.
- Boness, D. J., Chapman, P. J. & Mesnick, S. L. (2002) Life history and reproductive strategies. In: A. R. Hoelzel (ed.) *Marine Mammal Biology An Evolutionary Approach*, pp. 278–325. Blackwell Science Ltd., Malden, MA.
- Boness, D. J. (1991) Determinants of mating systems in the Otariidae (Pinnipedia). In: D. Renouf (ed.) *Behavior of Pinnipeds*, pp. 1–44. Chapman Hall, London.
- Born, E. W. & Knutsen, L. O. (1990) Satellite tracking and behavioral observations of Atlantic walrus (*Odobenus rosmarus rosmarus*) in NE Greenland in 1989. Teknisk rapport-Gronlands Hjemmestyre. Afdelingen for Levende Ressourcer. Nr. 20-oktober 1990: 68 pp.
- Bradbury, J. W. & Vehrencamp, S. L. (1977) Social organization and foraging in emballonurid bats. III. Mating systems. *Behavioral Ecology and Sociobiology* **2**, 1–17.
- Catchpole, C. K. (1987) Bird song, sexual selection and female choice. *Trends in Ecology and Evolution* **2**, 94–97.
- Clark, C. W. & Johnson, J. H. (1984) The sounds of the bowhead whale, *Balaenoptera mysticetus*, during the spring migrations of 1979 and 1980. *Canadian Journal of Zoology* **62**, 1436–1441.
- Cleator, H. J., Stirling, I. & Smith, T. G. (1989) Underwater vocalizations of the bearded seal (*Erignathus barbatus*). *Canadian Journal of Zoology* **67**, 1900–1910.
- Clutton-Brock, T. H. (1989) Mammalian mating systems. *Proceedings of the Royal Society of London* **B236**, 339–372.
- Clutton-Brock, T. H. & Albon, S. D. (1979) The roaring of red deer and the evolution of honest advertisement. *Behaviour* **69**, 145–169.
- Darling, J. D. & Berube, M. (2001) Interactions of singing humpback whales with other males. *Marine Mammal Science* **17**, 570–584.
- Davis, N. B. (1991) Mating systems. In: J. R. Krebs & N. B. Davies (eds.) *Behavioral Ecology* 3rd edn, pp. 263–299. Blackwell Scientific Publications, London.
- Davis, N. B. & Halliday, T. R. (1978) Deep croaks and fighting assessment in toads, *Bufo bufo*. *Nature (London)* **391**, 56–58.
- Deutsch, C. J., Haley, M. P. & Le Boeuf, B. J. (1990) Dominance rank and reproductive effort in male northern elephant seals, *Mirounga angustirostris*. *Canadian Journal of Zoology* **68**, 2580–2593.
- Emlen, S. T. & Oring, L. W. (1977) Ecology, sexual selection and the evolution of mating systems. *Science* **197**, 215–223.
- Falls, B. (1982) Individual recognition by sounds in birds. In: D. E. Kroodsma & E. H. Miller (eds.) *Acoustic Communication in Birds*. Vol. 2., pp. 237–278. Academic Press, New York.
- Fay, F. H. (1982) Ecology and biology of the Pacific walrus *Odobenus rosmarus divergens* Illiger. *North American Fauna* No. **74**.
- Fay, F. H., Ray, G. C. & Kibal'chich, A. A. (1984) Time and location of mating and associated behavior of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. NOAA Technical Report NMFS 12. pp. 89–99.
- Hartshorne, C. (1956) The monotony-threshold in singing birds. *Auk* **83**, 176–192.
- Hartshorne, C. (1973) Born to sing. *An Interpretation and World Survey of Bird Song*. Indiana University Press, Bloomington.

- Jarman, P. J. (1974) The social organization of antelope in relation to their ecology. *Behaviour* **48**, 215–267.
- Kessel, E. L. (1955) Mating activities of balloon flies. *Systematic Zoology* **4**, 97–104.
- Kiliaan, H. P. L. & Stirling, I. G. (1978) Observations on overwintering walruses in the eastern Canadian High Arctic. *Journal of Mammalogy* **59**, 461–463.
- Kroodsma, D. E. (1978) Continuity and versatility in bird song: support for the monotony threshold hypothesis. *Nature (London)* **274**, 681–683.
- Kroodsma, D. E. (1982) Learning and the ontogeny of sound signals in birds. In: D. E. Kroodsma & E. H. Miller (eds.) *Acoustic Communication in Birds. Vol. 2*, pp. 1–23. Academic Press, New York.
- Kroodsma, D. E., Bereson, R. C., Byers, B. E. & Minear, E. (1987) Use of song type by the chestnut-sided warbler: evidence for both intra- and inter-sexual functions. *Canadian Journal of Zoology* **67**, 447–456.
- Le Boeuf, B. J. (1991) Pinniped mating systems on land, ice, and in the water; emphasis on the Phocidae. In: D. Renouf (ed.) *Behavior of Pinnipeds*, pp. 45–65. Chapman and Hall, London.
- Le Boeuf, B. J. (1972) Sexual behavior in the northern elephant seal, *Mirounga angustirostris*. *Behavior* **41**, 1–25.
- Le Boeuf, B. J. & Reiter, J. (1988) Lifetime reproductive success in northern elephant seals. In: T. H. Clutton-Brock (ed.) *Reproductive Success*, pp. 344–362. University of Chicago Press, IL.
- Lindauer, M. (1961) *Communication Among Social Bees*. Harvard University Press, Cambridge, Mas.
- Maynard Smith, J. & Price, G. R. (1973) The logic of animal conflict. *Nature (London)* **246**, 15–18.
- Maynard Smith, J. & Price, G. R. (1976) The logic of asymmetric contests. *Animal Behaviour* **24**, 159–175.
- Miller, E. H. (1985) Airborne acoustic communication in the walrus *Odobenus rosmarus*. *National Geographic Research* **1**, 124–145.
- Morrice, M. G., Burton, H. R. & Green, K. (1994) Micro-geographic variation and songs in the underwater vocalization repertoire of the Weddell seal (*Leptonychotes weddellii*) from the Vestfold Hills, Antarctica. *Polar Biology* **14**, 441–446.
- Morton, C. S. (1977) On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist* **981**, 855–869.
- Noad, M. J., Cato, D. H., Bryden, M. M., Jenner, M. N. & Jenner, K. C. S. (2000) Cultural revolution in whale songs. *Nature (London)* **408**, p. 537.
- Nowicki, S. N., Stirling, I. & Sjare, B. (1997) Duration of stereotyped underwater vocal displays by male Atlantic walruses in relation to aerobic dive limit. *Marine Mammal Science* **13**, 566–575.
- Orians, G. H. (1969) On the evolution of mating systems in birds and mammals. *American Naturalist* **103**, 589–603.
- Parker, G. A. (1974) Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology* **47**, 223–243.
- Payne, K. (1991) A change of tune. *Natural History* **3**, 45–46.
- Payne, K., Tyack, P. & Payne, R. S. (1983) Progressive changes in the songs of humpback whales, *Megaptera novaeangliae*: a detailed analysis of two seasons in Hawaii. In: R. S. Payne (ed.) *Communication and Behavior of Whales*. Westview Press, Boulder, Col.
- Payne, R. B. (1979) Song structure, behaviour, and sequence of song types in a population of village indigo-birds, *Vidua chalybeata*. *Animal Behaviour* **27**, 997–1013.
- Payne, R. B. (1985) Behavioral continuity and change in local song populations of village indigo birds, *Vidua chalybeata*. *Zeitschrift für Tierpsychologie* **70**, 1–44.
- Payne, R. B. & Payne K. (1977) Social organization and mating success in local song populations of village indigo-birds, *Vidua chalybeata*. *Zeitschrift für Tierpsychologie* **45**, 113–173.
- Payne, R. S. & McVay, S. (1971) Songs of humpback whales. *Science (Washington, D.C.)* **173**, 585–597.
- Ray, G. C. & Burns, J. J. (1969) The underwater song of *Erignathus* (bearded seal). *Zoologica (N.Y.)* **54**, 79–83.
- Ray, G. C. & Watkins, W. A. (1975) Social function of underwater sounds in the walrus *Odobenus rosmarus*. In: K. Ronald & A. W. Mansfield (eds.) *Biology of the Seal: Proceedings of a Symposium, Guelph, Ont., August 14–17, 1972*. Rapp. P.-v. Réun. Cons. int. Explor. Mer, **169**: 524–526.
- Robertson, J. G. M. (1986) Female choice, male strategies and the role of vocalizations in the Australian frog, *Uperoleia rugosa*. *Animal Behaviour* **34**, 773–784.
- SAS Institute, Inc. (1988) *SAS User's Guide: Statistics*. SAS Institute, Inc., Cary, N.C.
- Schevill, W. E., Watkins, W. A. & Ray, C. (1966) Analysis of underwater *Odobenus* calls with remarks on the development and function of pharyngeal pouches. *Zoologica* **51**, 103–105.
- Sjare, B. (1993) Vocalizations and breeding behavior of Atlantic walruses in the Canadian High Arctic. Ph.D. thesis, University of Alberta, Edmonton AB, Canada.
- Sjare, B. & Stirling, I. (1996) The breeding behavior of Atlantic walruses, *Odobenus rosmarus rosmarus*, in the Canadian High Arctic. *Canadian Journal of Zoology* **74**, 897–911.
- Stirling, I. (1983) The evolution of mating systems in Pinnipeds. In: Eisenberg, J. F. & D. G. Kleiman (eds.) *Recent Advances in the Study of Behavior*. Special Publication No. 7. American Society of Mammalogists, Lawrence, KS.
- Stirling, I. & Sjare, B. L. (1988) Preliminary observations on the immobilization of male Atlantic walruses, *Odobenus rosmarus rosmarus*, with Telazol. *Mar. Mammal Science* **4**, 163–168.
- Stirling, I., Cleator, H. & Smith, T. G. (1981) Marine Mammals. In: I. Stirling & H. Cleator (eds.) *Polynyas in the Canadian Arctic*, Canadian Wildlife Series Occasional Paper No. 45. pp. 45–48.
- Stirling, I., Calvert, W. & Cleator, H. (1983) Underwater vocalizations as a tool for studying the distribution and abundance of wintering pinnipeds in the High Arctic. *Arctic* **36**, 262–274.
- Stirling, I., Calvert, W. & Spencer, C. (1987) Evidence of stereotyped underwater vocalizations of male Atlantic walruses, *Odobenus rosmarus rosmarus*. *Canadian Journal of Zoology* **65**, 2311–2321.

- Taigen, T. L. & Wells, K. D. (1985) Energetics of vocalization by an anuran amphibian, *Hyla versicolor*. *Journal of Comparative Physiology B* **155**, 163–170.
- Tinbergen, N. (1959) Comparative studies of the behavior of gulls (Laridae): a progress report. *Behavior* **15**: 1–70.
- Tyack, P. (1981) Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behavioural Ecology and Sociobiology* **8**, 105–116.
- Tyack, P. (1999) Communication and cognition. In: J. E. Reynolds III & S. A. Rommel (eds.) *Biology of Marine Mammals*, pp. 287–323. Smithsonian Institute.
- Wells, K. D. & Taigen, T. L. (1986) The effect of social interaction on calling energetics in the gray treefrog, *Hyla versicolor*. *Behavioural Ecology and Sociobiology* **19**, 9–18.
- Wells, R. S., Boness, D. J. & Rathbun, G. B. (1999) Behavior. In: J. E. Reynolds III & S. A. Rommel (eds.) *Biology of Marine Mammals*, pp. 324–423. Smithsonian Institute.
- Wilson, E. O. 1971. *The Insect Societies*. Harvard University Press, Cambridge, Mas.
- Winn, H. E. & Winn L. K. (1978) The song of the humpback whale, *Megaptera novaeangliae*, in the West Indies. *Marine Biology* **47**, 97–114.
- Zahavi, P. (1975) Mate selection—a selection for a handicap. *Journal of Theoretical Biology* **53**, 205–214.
- Zahavi, P. (1977) Reliability in communication systems and the evolution of altruism. In: B. Stonehouse & B. Perrins (eds.) *Evolutionary Ecology*, Macmillan Press, London.
- Zar, J. H. (1999) *Biostatistical Analysis*. Prentice Hall, Inc., Englewood Cliffs, N.J.