

Factors influencing the acoustic behaviour of male phocid seals

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Abstract

A series of natural history factors were examined to identify which are likely to influence acoustic behaviour in male phocid seals. Contrary to traditional thought, the degree of polygyny did not appear to influence vocal repertoire size or the other acoustic features examined. However, degree of sexual dimorphism, stability of the pupping substrate and density, guard-ability and predictability of oestrus females, and function of the signals, all appear to be important.

Species pupping in stable habitats tend to have vocalizations which are low in minimum frequency, whereas pack-ice breeders have vocalizations with high minimum frequencies. In species where oestrus females are predictably distributed and guardable (the southern elephant, *Mirounga leonina*, northern elephant, *Mirounga angustirostris*, grey, *Halichoerus grypus*, hooded, *Cystophora cristata*, and crabeater, *Lobodon carcinophagus*, seals) the acoustic displays of the males tend to be associated with male–male agonistic interactions and are likely to be intra-sexual in function. Male vocal repertoires tend to be simple in form composed of a reduced number of primarily broadband pulsed sounds following Morton's (1982) Motivational Structural Hypothesis.

However, in species where females do not remain hauled-out with their pups until weaning it is more difficult for males to physically guard them until oestrus. If oestrus females are inaccessible to males, either because they are moving to and from the sea or because they are widely distributed, males could use vocal displays to attract a mate. When oestrus females are widely and unpredictably dispersed long-range underwater advertisement displays are necessary (Scattergun advertizing). The acoustic displays of males of these species (leopard, *Hydrurga leptonyx*; Ross, *Ommatophoca rossii*; bearded, *Erignathus barbatus*; and ribbon, *Histiophoca fasciata*, seals) must travel long distances. Sounds that are required to travel over long distances could change slightly in character due to the differing propagation characteristics of the varying fre-

quency components within the vocalization. The signal also could be masked by background noise. Perhaps it is easier for a listening seal to recognise a smaller number of stereotyped vocalizations. Therefore, these seals tend to have fewer, narrowband, highly stereotyped sounds used in stylized repetitive displays which helps ensure that the signal is recognized by a receiving seal at a distance.

In species where oestrus females are predictably distributed, but unguarded (Weddell, *Leptonychotes weddellii*; harp, *Pagophilus groenlandicus*; harbour, *Phoca vitulina*; and ringed, *Phoca hispida* seals) males perform shorter-range underwater advertisement displays. The signals of species advertizing to a local audience are not constrained by propagation difficulties. These species therefore adopt a large array of sound types, and include subtle variations of the same sound type, greatly increasing their overall repertoire size (Local advertizing).

Key words: phocid seals, acoustic behaviour, mating systems, predictable guardable oestrus females, sexual selection.

Introduction

A correlation between a highly polygynous breeding system and large vocal repertoire size was postulated for pinnipeds by Evans & Bastian (1969). This theory was subsequently supported by Thomas & Stirling (1983) who noted that gregarious polygynous species have more highly developed sound repertoires than seals that are distributed in serially monogamous pairs or at low breeding densities. This relationship also was supported by Cleator *et al.* (1989) who noted that the highly polygynous Weddell and harp seals had larger repertoires than solitary species, such as the crabeater, Ross, ribbon, hooded and bearded seals. Furthermore, the more gregarious subspecies, the Ladoga ringed seal (*Phoca hispida ladogensis*), has a greater repertoire size compared to the usually solitary subspecies the Saimaa ringed seal, *Phoca hispida saimensis* (Kunnasranta *et al.*, 1996).

On broader examination of the phocid seals; however, there is a departure from this pattern. The leopard seal, a species distributed at low densities, has at least 12 different underwater social sounds (Stirling & Siniff, 1979; Thomas & Golladay, 1995; Rogers *et al.*, 1996) not including the clicks and buzzes described by Thomas *et al.* (1982). In comparison, the highly polygynous harp seal has only 18 sound types (Møhl *et al.*, 1975; Watkins & Schevill, 1979; Terhune & Ronald, 1986). Furthermore, both elephant seal species are highly polygynous, yet their vocal repertoires are small and the sounds simple. There does not appear to be a clear relationship between vocal repertoire size and degree of polygyny in the phocid seals.

The phocid seals provide an excellent model to compare signal structure and variation, and to examine the relationship between signal structure and the behaviour of communication (Miller, 1991). Phocid social systems are diverse, including large dense breeding concentrations on ice or land, dispersed parturient females attended by mates, aquatic and terrestrial territoriality and dominance hierarchies. Although all phocids can be considered to be potentially polygynous, the distribution of females affects the degree to which polygyny has developed (Le Boeuf, 1991).

However, a paucity of information makes it difficult to understand the development of acoustic behaviour in phocids. The acoustic behaviour of some species, such as the elephant and Weddell seals, have been examined extensively, whereas for others, particularly the pack ice seals, there is little or no information.

To date, the mating system has been the only factor considered as an influence on the development of vocal repertoire size, yet other factors could mould the type of acoustic display that develops. These factors could be interlinked. Other factors likely to play a role in the development of phocid acoustic behaviour are: distribution of females during breeding, predictability of finding a mate, stability of the pupping platform, degree of foraging during lactation, sexual selection, spatial distribution, and the physical environmental characteristics such as propagation distance, propagation characteristics, and background noise. There does not appear to be a simple relationship between repertoire size and mating system. In this discussion paper, the influence of seven factors on the development of phocid acoustic behaviour will be examined including: (a) degree of polygyny, (b) degree of sexual dimorphism including weight and length, (c) density during the breeding season, (d) stability of the pupping platform, (e) duration of lactation, (f) number of days that males cannot gain access to females, and (g) predictability of males accessing females.

Materials and Methods

Acoustic variables

The acoustic variables are repertoire size and four acoustic features—minimum frequency, maximum frequency, frequency bandwidth, and total duration.

Repertoire size—The number of vocalization types produced by the males of each phocid species was taken from the literature. Cow, pup, and surface calls were not included. Because the social context was not known for many of the sounds, both social sounds and those produced as part of breeding displays were included. Geographic variation has been shown in many species and there have been different levels of study conducted within different regions. Therefore, the upper number of vocalizations described for any region has been allocated as the species repertoire size. Some researchers tend to be ‘splitters’, describing many different variants of a sound type. There is great variability in acoustic characteristics which could reflect inter-individual, age-related or motivational variations. Other researchers are ‘lumpers’, describing sound types as a group that encompasses the variation seen. I tend to be a ‘lumper’ so the literature has been compared from a lumpers’ perspective.

Bearded seals are allocated as having six underwater sound types, Cleator *et al.* (1989) described five trills from seals in Alaska; six in Ramsay Island; four in Hudson Bay; three in Baffin Island; two in Dundas Island; and six in Table Island. Other researchers described three in the Canadian Arctic (Terhune, 1999); and four in Svalbard (Van Parijs *et al.*, 2001).

Crabeater seals are allocated as having only the one call, the groan, as described by Stirling & Siniff (1979) and Thomas & DeMaster (1982). This is the only described call for this species; however, there has been very little acoustic work conducted on the crabeater seal.

Grey seals are allocated as having four types of male calls (Asselin *et al.*, 1993): the roar also called the male roar (Schneider, 1974), the growl also called the humm or moan (Schusterman *et al.*, 1970), the wail (Schneider, 1974) or hoot (Hewer, 1957; 1960) and the trot also called the jackhammer sound (Schneider, 1974). Calls that have not been included are: clicks and those produced as part of maze experiments for the grey seal (Oliver, 1977); those produced by females, the rup and rupe (Asselin *et al.*, 1993), and those produced by unknown sexed seals including clicks and knocking (Asselin *et al.*, 1993).

Harbour seals are allocated as having five vocalizations in California (Hanggi & Schusterman,

1994), one type in Moray Firth, and two types in Orkney (Van Parijs *et al.*, 2000a).

Harp seals are allocated as having 18 call types. Møhl *et al.* (1975) described 16 call types from seals in Canada. Eighteen sound types were described from seals in Jan Mayen, Canada; 18 in St. Lawrence (Terhune, 1994; Perry & Terhune, 1999) and 18 from captive seals (Serrano, 2001).

Hawaiian monk seals, *Monachus schauinslandi*, are allocated as having four call types (Miller & Job, 1992).

Hooded seals are allocated as having three call types. They are described as having variations on one call type in Magdalen Islands, Quebec (Terhune & Ronald, 1973). Ballard & Kovacs (1995) described three orders of sounds, although these were then divided further into five call types with eight subcategories using cluster analysis. Examination of sonograms in the publication; however, identified a high degree of variability in a few sound types.

Leopard seals are allocated as having 12 sound types. Four sounds around the South Shetland Islands (Stirling & Siniff, 1979), 12 sounds in Eastern Antarctica and captive seals (Rogers *et al.*, 1995), five calls at McMurdo Sound and nine calls at Palmer Peninsular (Thomas & Golladay, 1995). Ultrasonic sounds produced by leopard seals chasing fish in the dark (Thomas *et al.*, 1982) are not included.

Northern elephant seals are allocated as having three sound types. Bartholomew & Collias (1962) described elephant seals as having three sound types; Shipley *et al.* (1981) described two; and Shipley *et al.* (1986) described three.

Ribbon seals are allocated as having four sound types (Watkins & Ray, 1977).

Ringed seals are allocated as having six sound types all produced by the Ladoga ringed seal in Valaam Archipelago (Kunnsaranta *et al.*, 1996).

Ross seals are allocated as having three sound types (Watkins & Ray, 1985).

Southern elephant seals are allocated as having one sound type (Sanvito & Galimberti, 2000).

Weddell seals are allocated as having 34 sound types. They are described to have 12 in-air call types by Terhune *et al.* (1993); 34 underwater call types divided into 12 call categories in the McMurdo region (Thomas & Kuechle, 1982) and 21 underwater call types in Palmer Peninsula (Thomas & Stirling, 1983); 49 underwater call types divided into 13 call categories in the Davis region although only 20 of these sound types were heard more than infrequently (Pahl *et al.*, 1997).

Acoustic features—Where frequency and temporal values were given by authors mentioned above

(repertoire size) the mean values were used for each sound type. Only the standard acoustic variables: minimum frequency, maximum frequency, frequency bandwidth and total duration were used. For narrowband sounds both the minimum and maximum frequencies are given as the fundamental frequency therefore there is no bandwidth measurement.

Predictor variables

The predictor variables are: (a) degree of polygyny, (b) degree of sexual dimorphism including weight and length, (c) density during breeding season, (d) stability of birthing platform, (e) length of lactation, (f) number of days males have no access to females, and (g) predictability of female oestrous.

Degree of polygyny (polygyny)—The degree of polygyny has been coded following the categorical classification of mating systems described by Riedman (1990): 4=extreme polygyny (mating with at least 15 to 20 females); 3=moderate polygyny; 2=slight polygyny and 1=serial monogamy (Table 1). Although all seals could be considered to be polygynous, in widely dispersed species with short mating seasons and where males remain in attendance with lone females until oestrus, there will be little opportunity for males to find a second oestrus female. These seals have been referred to as serially monogamous.

Degree of sexual dimorphism—Body lengths (length) and body weights (weight) were gathered from Bininda-Emonds & Gittleman (2000). Dimorphism was calculated as log male size/female size, this equals log male size – log female size (Lindenfors *et al.*, 2002) (Table 1).

Density during the breeding season (density)—The density has been coded following a categorical classification where 1=widely dispersed; 2=small groups; 3=moderate sized groups and 4=large groups (Table 1).

Stability of haulout platform during breeding (stability)—The stability of the haulout platform during breeding was coded following a categorical classification where 1=pupping on pack ice; 2=pupping on fast ice and 3=pupping on land (Table 1). The rationale for ordering the pupping platforms from land to pack-ice comes from the degree of stability of these regions. Pupping on land is incredibly stable, fast-ice habitat is a moderately stable ice environment but is not as stable as land, and the pack-ice is an unstable platform which is continuously breaking-up through the breeding season.

Table 1. Predictor variables.

Seal species	Polygyny	Weight	Length	Density	Stability	Lactation	Days No access	Female predictability	References
Bearded Grey	1	-0.01823	0	1	1	24	23	1	Kovacs, 2002
Harbour	3	0.177024	0.079884	3	3	18	0	3	Hall, 2002
Hawaiian monk	2	0.083546	0.023065	3	3	24	12	2	Burns, 2002
Hooded	2	-0.1852	-0.03784	2	3	42	0	3	Gilmartin & Forcada, 2002
Ribbon	1	0.188192	0.101106	1	1	4	0	3	Kovacs, 2002
Harp	1	0.071768	-0.0048	1	1	25	5	1	Fedoseev, 2002; King, 1983
Ringed	2	0.018064	0.016856	3	1	12	9	2	Lavigne, 2002
Northern Elephant	1	0.032516	0.001346	1	2	42	10	2	Miyazaki, 2002; Riedman, 1990
Southern Elephant	4	0.646864	0.18339	4	3	27	0	3	Hindell, 2002
Leopard	4	0.843739	0.237953	4	3	23	0	3	Hindell, 2002
Weddell	1	-0.05412	-0.05062	1	1	30	28	1	Rogers, unpublished data
Ross	3	-0.01889	-0.0162	3	2	49	27	2	Thomas, 2002
Crabeater	1	-0.02712	-0.03278	1	1	28	27	1	Thomas, 2002
	1	-0.00684	-0.00478	1	1	28	0	3	Bengtson, 2002

Polygyny: 4 = extreme polygyny (mating with at least 15 to 20 females), 3 = moderate polygyny, 2 = slight polygyny and 1 = serial monogamy; Weight: log male weight—log female weight; Length: log male length—log female length; Density: 1 = widely dispersed, 2 = small groups, 3 = moderate sized groups and 4 = large groups; Stability: 1 = pupping on pack ice, 2 = pupping on fast ice and 3 = pupping on land; Days no access: the number of days to oestrus (Riedman, 1990) minus the number of days after parturition that females return to the water, presumably to forage (reference); Female predictability: 1 = low predictability, 2 = medium predictability and 3 = high predictability.

Duration of lactation (lactation)—The length of lactation in days is used and the reference for each species is given in Table 1.

Days males have no access to females (days no access)—Females come into oestrus near the end or at the end of lactation, therefore if a cow has returned to the sea prior to oestrus it decreases the accessibility of males to those females. The number of days that the male will not have access to hauled-out females (days no access, Table 1) has been calculated as the number of days from parturition to oestrus (Riedman, 1990) minus the number of days after parturition that females return to the water (reference Table 1). Where the actual number of days after parturition that females return to the water is not specified (ringed and ribbon seals), but a report of late lactation is given, an estimate of 75% of the lactation period is used. There is little information on the reproductive behaviour of the Ross seal as it is rarely seen.

Predictability of females oestrous (female predictability)—The ability of a male to predict an oestrus cow was coded following a categorical classification: 1=low predictability, where the movement of the cows is unpredictable both in space and time because cows pup singly in the drifting pack-ice and there is no attending male (e.g., leopard seal); 2=medium predictability, where cows forage through lactation and there is no attending male, yet the cows travel to and from haul-out and feeding grounds along a predictable route at the time of oestrus (e.g., Weddell seal); and 3=high predictability, where cows remain with their pups until they come into oestrus and there is an attending bull (e.g., southern elephant seal, Table 1).

Statistics

Various analysis techniques were used depending on the type of response variable. Log-linear modelling, assuming a Poisson distribution for the response variable repertoire size and estimates of parameters adjusted by a dispersion parameter, was used to ascertain if there was a relationship between the number of calls a species produces and any of the seven predictor variables. Multiple regression analysis was used for the acoustic variables, minimum frequency, maximum frequency, bandwidth and duration, to ascertain the best predictors for each feature. It does not identify any underlying causal mechanisms. Log 10 values of the acoustic variables were used in the analysis to correct for non-normal distribution and outliers. The magnitude of the standardized regression coefficients (Beta values) allows the comparison of the relative

contribution of each independent variable in the prediction of the dependent variable.

Results

Repertoire size

Four significant predictors were found to describe repertoire size via stepwise regression (and confirmed using backwards elimination): days no access ($P<0.001$), density ($P<0.001$), and stability ($P=0.001$) were all positively related whereas weight ($P=0.008$) was negative related. Therefore, species where the males do not have access to oestrus females for long periods, breed in high densities and in stable environments tend to have more calls in their repertoire. Whereas, species with reverse size dimorphism have more calls.

Minimum frequency

There was a significant relationship (Table 2) where weight, stability, and lactation are the most important predictors of minimum frequency; however, only stability was significant (Table 2). The regression coefficient for stability was negative; therefore, species that pup in unstable habitats tend to have vocalizations with higher minimum frequencies.

Maximum frequency

There was a significant relationship (Table 2) where density, days with no access, and female predictability are the most important predictors of maximum frequency; however, only female predictability was significant (Table 2). The regression coefficient for female predictability was positive; therefore, species with oestrus females in predictable locations tend to have vocalizations with higher maximum frequencies.

Frequency bandwidth

There was a significant relationship (Table 2) where density, lactation, days with no access, and female predictability are the most important predictors of frequency bandwidth; however, only no access and female predictability were significant (Table 2). The regression coefficient for no access was negative and for female predictability positive. Therefore, longer males do not have access to oestrus females, because they are foraging, the more likely they are to have vocalizations with narrow frequency bandwidths. However, if oestrus females are highly predictable, then they tend to vocalise with broad frequency bandwidths.

Total duration

There was a significant relationship (Table 2) where polygyny, length, and days with no access are the most important predictors of total duration; however, only length and days with no access were

Table 2. Results of multiple regression analysis, significant values are bolded.

Response variables	Multiple R	F-value	d.f.	P-value	Predictor variables—beta							
					Degree polygyny	Body weight	Body length	Breeding density	Habitat stability	Lactation length	Days no access	Female oestrous predictability
Minimum frequency	0.355829	3.443036	8190	0.001001	0.01	0.44	0.239	0.224	-0.309	0.375	-0.19	-0.06
Maximum frequency	0.381719	4.050856	8190	0.000181	0.233	-0.19	-0.29	-0.38	0.01	0.293	-0.36	-0.379
Frequency bandwidth	0.413154	4.322452	8168	0.000093	0.319	-0.26	-0.19	-0.54	-0.09	0.364	-0.42	-0.36
Total duration	0.534642	8.105074	8162	0.000001	-0.94	-0.47	1.66	0.357	-0.12	0.467	0.973	-0.13

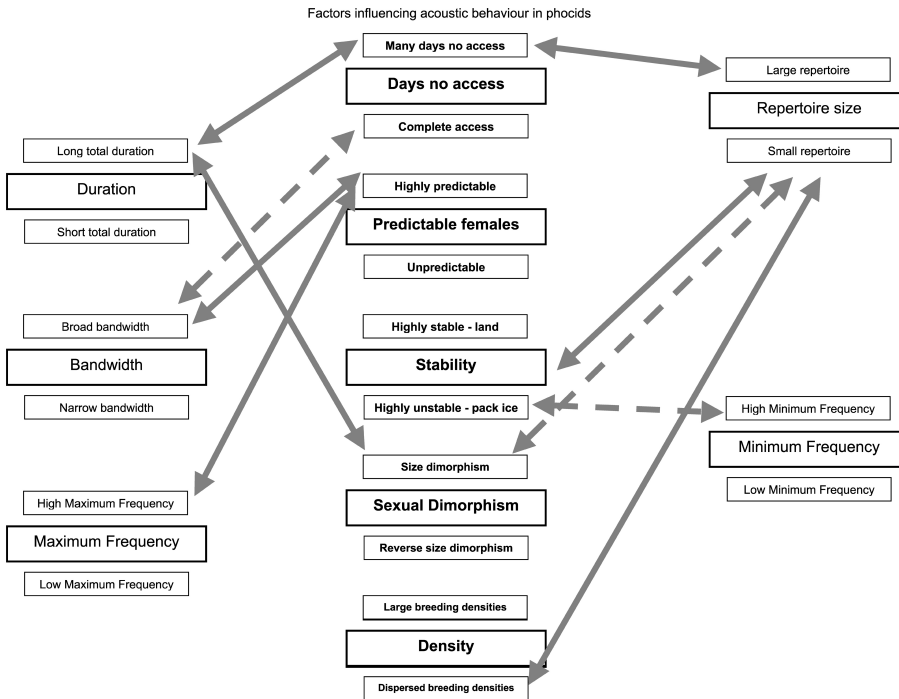


Figure 1. Predictor variables influencing the characteristics of the vocal behaviour of male phocid seals. Solid lines indicate positive relationships, dashed lines negative relationships.

significant (Table 2). Both the regression coefficient for length and days with no access were positive; therefore, species where males are substantially larger than the females and/or do not have access to oestrus females, because they are foraging, are more likely to have longer duration vocalizations.

Discussion

Degree of polygyny

Contrary to traditional thought, the degree of polygyny of a species does not appear to influence phocid repertoire size, or any of the other acoustic features studied herein. Phocid species, displaying extreme ranges of polygyny, share similar acoustic repertoires, both in the number of calls and types of sounds. For example, males of both the highly polygynous northern and southern elephant seals and the serially monogamous crabeater and hooded seals produce broadband pulsed vocalizations in their limited repertoires.

Density

The breeding density appears to positively influence the repertoire size. Species breeding at high densities have more calls in their repertoire than species breeding at low densities. In pinnipeds, the degree of polygyny and breeding density are highly influ-

enced by ecological factors (Stirling, 1975; 1983). In phocids, there is no male parental care of the young so a male's reproductive success will be limited by his access to females, either by his ability to attract or dominate a potential female partner or partners; and/or his ability to dominate rival males (Stirling, 1983). Both degree of polygyny and density are driven directly by the distribution of the cows during breeding (Emlen & Oring, 1977).

Degree of sexual dimorphism

Degree of sexual dimorphism appears to influence the repertoire size and total duration of calls (Fig. 1). Sexually dimorphic species in which the males are heavier than the females have fewer vocalizations and species in which males are longer than females tend to produce longer vocalizations than monomorphic or reverse size dimorphic species. Sexual dimorphism, where males are larger than females, is common in pinnipeds and the most extreme example is the southern elephant seal where males are up to seven times longer than females. Monomorphism, where both sexes are the same size, and reverse sexual dimorphism, where females are larger than males, are common in aquatically mating seals. In species that mate aquatically, there is less advantage for males to be larger than females because the males have limited ability to

monopolise females. In addition, the smaller size could enhance the male's agility in the three-dimensional environment, whereas larger size enhances a female's ability to provide larger quantities of fat-rich milk to their pups (Mesnick & Ralls, 2002).

Stability of the haulout substrate during breeding

Stability of the pupping substrate appears to influence the repertoire size and the minimum frequency. Phocid cows give birth on diverse breeding habits: on stable inter-tidal sand bars and rocky beaches; on relatively stable fast-ice attached to land; and on unstable floating pack ice (Kovacs & Lavigne, 1986; Lydersen & Kovacs, 1999). Species pupping on land and fast ice tend to have more vocalizations which are low in minimum frequency, whereas pack-ice breeders have fewer vocalizations with high minimum frequencies (Fig. 1). The ice floes of the pack ice provide a highly unstable pup-rearing environment because the floes are continuously breaking-up through the breeding season. Most pack-ice-breeding seals are widely dispersed and therefore, need to communicate over long distances. As sound propagates through the ocean there is some distortion of the signal due to frequency-dependent transmission or interference of arrivals by multi-path propagation (Urick, 1983). This distortion could corrupt information contained within the original signal. Consequently, repeating a few stylized vocalization types could aid receivers with recognition of a call when the signal-to-noise ratio is poor, which is common when individuals are at a significant distance. Many of the pack-ice seals vocalise for many hours and have few stylized calls, perhaps providing redundancy. Signals also are subject to masking by environmental noise (Brenowitz, 1986; Mercado & Frazer, 1999), which also will influence the distance at which a sound can be detected. Masking noise can be generated by physical processes such as wind, sea state or precipitation, or by the vocalizations of conspecifics (Wiley & Richards, 1982; Klump, 1996). Harp seals are gregarious, unlike other pack-ice seals; however, they still have high calling rates. A harp seal herd produces a continuous broadband sound that might mask an individual's vocalizations (Terhune & Ronald, 1986).

As low frequency sounds propagate longer distances under water you would assume that the pack-ice breeders would have vocalizations with lower minimum frequencies than the vocalizations of species breeding in stable habitats. However, this was not the case in these findings and may be an artifact of the data set used in this study. In the analysis, both social sounds and breeding display sounds were included for each species. This was done because the social context has not been con-

firmed for many vocalizations so it was uncertain whether they were social sounds or breeding display sounds. The agonistic social sounds of mammals tend to be broadband with low minimum frequencies (Morton, 1982). This has been found to be the case for the leopard seal (Rogers *et al.*, 1996), one of the few pack ice breeding species where the vocal repertoire has been studied within a behavioural context. Leopard seal social sounds tend to be lower in minimum frequency than their sounds used as part of their breeding display (Rogers *et al.* 1996). Species breeding in stable environments, on land, and on fast ice, tend to clump together, so there is greater opportunity for researchers to record agonistic acoustic encounters between seals. These sounds tend to be broadband, low minimum frequency sounds. By contrast, studies of the acoustic behaviour of the pack-ice breeders have centered on their breeding displays and less on their social sounds. This is because there are fewer opportunities for researchers to record the rarely seen interactions between individuals in these widely dispersed species. In addition, the enormous logistic constraints of studying seals within the pack ice compound the difficulty of recording these opportunities. It is likely that fewer social sounds have been described from the pack ice species. It is possible that if social sounds had been removed from the data set and only the breeding display sounds had been compared that the pack-ice species may have lower minimum frequency vocalizations in keeping with their improved propagation characteristics.

Duration of lactation

Duration of lactation does not appear to influence the phocid repertoire size, or any of the other acoustic features studied herein.

Degree of accessibility of oestrus females

The degree of accessibility that males have to oestrus females appears to influence their repertoire size, and the total duration and frequency bandwidth of their calls. Cows mate either prior to or after the time that they wean their pups (Stirling, 1983; Boness & Bowen, 1996) and will not be receptive to males until they enter oestrus. If cows fast through lactation, they remain with their pups and do not leave the breeding area until weaning. Attending males can forcibly coerce oestrus females to mate on land before they depart from the breeding area in the elephant and grey seals (Le Boeuf & Mesnick, 1990), or once the females enter the water in aquatic mating crabeater and hooded seals. Therefore, oestrus females are highly accessible to any attending males. Species where males have greater access to oestrus females tend to have small vocal repertoires composed of short duration,

broadband sounds (Fig. 1). Although the elephant and grey seals and the hooded and crabeater seals display opposing degrees of polygyny and density, both share the same extremely high level of accessibility to oestrus females. In both groups, the cows fast through lactation, remain with their pup and are attended by males. The males of these species actively compete with one another limiting other male's access to the female(s) within their region. Whereas, elephant and grey seals defend large numbers of females, crabeater and hooded seal males defend only a single lactating females and her vicinity. Crabeater seal males can surround ice floes where a triad of seals, a cow her pup and an attending male, have hauled-out. The surrounding males actively compete with one another, and the guarding male, for access to the oestrus female. If a superior male, the attending male remains with the cow and her pup until the pup has weaned and the cow comes into oestrus. The male can actively try to force the pup away from the cow. There is a great deal of inter-sexual aggression as the cow maintains herself between the bull and her pup (Shaughnessy & Kerry, 1989). After the pup has weaned, it is presumed that the attending male mates with the oestrus female as she enters the water. Therefore, it is not surprising that such species produce short-duration, broadband sounds because these sounds are typical of vocalizations used in agonistic, predominately aggressive, displays by a wide range of species (Morton, 1982).

Where males have limited access to monopolise or guard pre-oestrus females these species tend to have large vocal repertoires composed of long duration, narrower-band sounds (Fig. 1). Previously, all phocid cows were believed to fast through lactation; however, it has been shown recently that many phocids forage or leave the breeding area prior to their pup weaning (Bowen *et al.*, 2002) therefore, becoming less accessible to males. Late in lactation, but prior to oestrus, female harbour seals leave their pups ashore and return to sea to forage (Bowen *et al.*, 1992; Boness *et al.*, 1994). Where females are widely dispersed during the mating season it is unlikely to be economical for males to monopolise females (Thompson *et al.*, 1994). Males have less ability to physically overpower or monopolise females moving freely in the three-dimensional aquatic environment therefore, if females enter the water before coming into oestrus males will have limited access to oestrus cows. Species where it is difficult for males to monopolise or guard pre-oestrus females include the fast-ice breeding species, the Weddell and ringed seals, pack-ice breeders the bearded, harp, ribbon and leopard seals, and the land-breeding harbour seal. Although breeding in different habitats and displaying mating systems from moderately polygynous to

serially monogamous they all share a low degree of access to oestrus females.

Predictability of males finding oestrus females

Predictability of oestrus females appears to influence the bandwidth and maximum frequencies of calls. Female distribution during the breeding season ranges from high concentrations of elephant and grey seals, to more widely dispersed pack-ice breeding seals, the leopard, bearded, crabeater and hooded seals. Distribution of the cows during pupping and lactation will depend on the stability of the habitat, the duration of lactation, and whether females forage through lactation. However, it is ultimately the predictability of the distribution of the cows during the time of oestrus which will influence the male's accessibility to potential mates.

Species which have predictably distributed oestrus females tend to have broadband sound types with high maximum frequencies and large bandwidths (Fig. 1), again characteristics of agonistic displays. In these species, females remain hauled-out with their pups until oestrus and have attending males. The males have not only a high level of accessibility to oestrus females, but these females are predictably distributed. This group includes species at opposite degrees of polygyny and density, but they share the same predictable access to oestrus females, as well as having no period when there will be no access to females.

Where males have limited ability to guard pre-oestrus females, either because cows forage through lactation or have gone to the water for predator avoidance prior to oestrus, males have varying levels of potentially encountering oestrus females corresponding with the predictability of the cows behaviour. In some species, females are not accessible to be guarded by attending males, yet females are relatively predictable in their distribution, as cows travel to and from a predictable site. In the stable Antarctic fast-ice, small to moderate groups of female Weddell seals breed in clumps in predictable areas where there is reliable access to and from the water through breathing holes in the ice. Females use these same breathing holes as they travel back and forth between their haul-out and feeding sites. Male Weddell seals vocalize under water in the vicinity of the breathing holes so they can predictably encounter large groups of females. Similarly, female harbour seals pup in a very stable habitat, even if on land, and show strong site fidelity. Females travel along predictable routes when swimming back and forth between their foraging grounds and their pups left at the haul-out sites (Van Parijs *et al.*, 1997). Consequently, harbour seal males have highest densities in areas where female densities are the greatest (Van Parijs *et al.*, 1997; 1999). Males conduct display-dives on

the female feeding grounds farther out to sea and along their transit routes (Van Parijs *et al.*, 1997; 1999; 2000b). By contrast, the females of some species are neither accessible to be guarded by males nor have a predictable distribution at the time of oestrus. All these species pup on the drifting floes of the pack ice and do not have attending males. Because the females either forage through lactation or go to the water prior to oestrus, it is energetically inefficient for males to remain in attendance. Species in which males have low predictability of encountering oestrus females tend to produce narrowband sounds of low minimum frequency and narrow bandwidths (Fig. 1). Pack-ice species are solitary and therefore, the cows are dispersed widely. Seals that breed on pack ice are not forced to clump together as the cows have a vast expanse of ice that offers protection from predators and easy access to food. In addition, the pack ice is a mobile environment. Floes are continuously moving with the wind and currents. Ice floes drift up to 20 km per day in some areas of the Antarctic (Heil & Allison, 2001). The position of these mobile cows at the time of oestrus is completely unpredictable. Because the pack ice species have short lactation periods, and likely synchronized pupping and oestrus, it is improbable that males can predictably find a large number of these isolated females who come into oestrus at roughly the same time. Consequently, Van Parijs *et al.* (2001) noted that the distribution of male bearded seals was not correlated with the distribution of the females, but was greatest around fjord entrances. To intercept passing females, the males produce underwater vocalizations as part of a stylized display in geographical bottlenecks, such as fjord entrances (Van Parijs *et al.*, 2001). However, in the Antarctic pack ice there are no such bottlenecks therefore, it is not probable for males to wait for females in any particular position. Lone male leopard, bearded, Ross and ribbon seal males call under water for long periods during the breeding season. These species tend to produce stylized trill-like sounds.

Sexual selection

A driving force in the development of acoustic behaviour in birds is whether their display has an inter-sexual function, is used to attract females, or has an intra-sexual function, is involved in male-male agonistic displays (Catchpole, 1982). It is tempting to speculate that sexual selection is also the cause for the development of male vocal repertoires in phocids. Limited repertoires have developed in species where there is extensive access to oestrus females with displays primarily associated with intra-sexual competition. In contrast, elaborate repertoires have developed in species where there is little access to oestrus females and their

displays can operate to attract oestrus females, an inter-sexual function. However, due to the paucity of information about the function of their calls, particularly those of the aquatic-mating species, it is impossible to know at this time.

Intra-sexual male-male agonistic displays

The highly polygynous species, the elephant and grey seals, as well as the slightly monogamous crabeater and hooded seal, all have poorly-developed vocal repertoires composed of few, broadband sounds with few elements. Their acoustic displays are associated primarily with male-male agonistic behaviour (intra-sexual competition). All have females that are highly accessible and predictably distributed so that males can easily monopolise and guard them. The males exercise direct choice of a mate, whereas females have less choice because they are less able to reject an unwanted suitor. In the gregarious elephant and grey seals, males can forcibly coerce females to mate because they both mate on land, where phocid seals are not agile, and the females are significantly smaller than the males. However, females can exercise choice indirectly. During mating, females vocalize and these calls presumably incite male-male competition; the female is then mated with the successful bull. Calling therefore, ensures that she was mated by a physically superior male. In the solitary hooded and crabeater seals, males guard a single female, and this male will most likely mate with the female when she comes into oestrus. The attending male is likely to be physically superior because he has defended his position over a period of time from rival males attempting to gain access (Fedak *et al.*, 2002). These contests between rival males result in a great deal of close-range agonistic behaviour. Females are widely dispersed; therefore, having a well-developed loud acoustic display would only alert other males to the position of 'his' pre-oestrous or oestrus female. Therefore, the primary focus of the simple acoustic display of these seals, which have diverse mating systems, appears to be male-male competition, either in the guarding of a territory with its cows (elephant and grey seals) or directly guarding a single cow (crabeater and hooded seals).

Inter-sexual female attraction displays

Where males cannot monopolise oestrus females, either because they are moving through the water to and from fixed positions (Weddell, harbour, ringed and harp seals) or because they are unpredictable and widely distributed (leopard, Ross, bearded, and ribbon seals), males tend to have elaborate vocal displays. Perhaps their displays are primarily to attract oestrus females, inter-sexual function, because males cannot maximize their reproductive success by resource defence or physically securing

females. The females have greater opportunity to exercise mate choice so males can use their loud repetitive calls to attract oestrus cows (Le Boeuf, 1991). Elaborate male displays could advertise information about maturity, learning skills, behavioural versatility, and responsiveness (Miller, 1991). In many of these species, lone individual males perform stereotypic vocal and dive displays under water in well-defined aquatic territories, i.e., in the leopard seal (Rogers & Cato, 2002), harbour seal (Van Parijs *et al.*, 2000a), and the bearded seal (Van Parijs *et al.*, 2001). Leopard seal males call under water and then rest at the water surface in alternating 2-min cycles. Calling continues for many hours each day from late October through to early January (Rogers & Cato, 2002). The female leopard seals also calls under water, but only while in oestrus (Rogers *et al.*, 1996). In captive leopard seals, a male and female called back and forth to one another prior to copulation (Marlow, 1967; Rogers, unpublished data). Perhaps the acoustic displays of the males serve to indicate their fitness because it requires energy and good health to produce these prolonged displays, and time spent calling is time away from foraging and resting. This cost could be reflected in changes in body condition. Male harbour seals can lose up to 25% of their body weight during the breeding season. Acoustic displaying increases during the breeding season in many phocids, including the ringed seal (Stirling, 1973), harp seal (Møhl *et al.*, 1975; Turnbull & Terhune, 1993), harbour seal (Hanggi & Schusterman, 1994; Bjorge *et al.*, 1995; Van Parijs *et al.*, 1999) and the leopard seal (Rogers *et al.*, 1996).

The elaborate displays of males may not only advertise superior status to the females, but also to other males. It would be advantageous to minimize the number of rival males in the area. Male harbour seals interrupt vocalizing bouts to fight with other males that swim into their vocalizing area. The underwater vocal displays, in conjunction with their visual displays, are believed to be used in male-male competition (Hanggi & Schusterman, 1994). Similarly, some calls used by male Weddell seals have an agonistic function (Thomas & Kuechle, 1982). It is likely that their displays have a dual function, both to attract oestrus females and repel rival males.

Where oestrus females (although not guardable) are highly predictable in distribution, males can advertise to a known 'target' audience of females. In contrast, in species where oestrus females are widely and unpredictably dispersed, males need to advertise broadly in a 'scattergun' approach. The males of each group have vastly different advertising ranges and therefore, different communication requirements. Males of the predictably distributed species the Weddell, harp, harbour and ringed seals,

only need a short-range underwater advertisement display, which they perform in the vicinity of potentially oestrus females. Male Weddell seals perform their underwater acoustic-dive displays around breathing holes used by females as they travel to and from their pups and the feeding grounds. Communicating in the near-field means that these seals are not restricted to produce sounds constrained by signal propagation needs. Many different sound types can be used, as well as subtle variations of different sound types. Male Weddell seals have a large array of different sound types, up to 34 in some regions, but Weddell seals can be heard for long distances.

Males of the widely dispersed, unpredictable species the leopard, Ross, bearded, and ribbon seals, need to produce long-range underwater advertisement displays to attract oestrus females. As discussed, the propagation of sound through the ocean occurs with some distortion of signal, such as loss of frequency-dependent transmission or interference of arrivals by multi-path propagation (Urlick, 1983). This would tend to corrupt information contained in the sound characteristics. Because propagation conditions and masking by background noise can reduce the detectability of vocalizations at a distance, having fewer, highly stereotyped, low frequency vocalizations could enhance the likelihood of vocalizations being recognized by a seal listening at a distance. These seals tend to produce narrower band sounds, trills or trill like sounds, as part of their vocal repertoires. They tend to vocalize over long periods, continuing over many hours with repetition providing significant redundancy of the signal. This could aid in recognition when the signal-to-noise ratios are poor. This is known to be the case for birds, where repetition and redundancy within territorial songs of many birds assure transmission of information in order that the message can be received (Becker, 1982).

In conclusion, there appears to be three groups of phocid seal vocalization strategies. The acoustic displays of the first group, the elephant, grey, crabeater and hooded seals; are small and composed of broadband noisy pulsed sounds which tend to be agonistic in function. The second group; the leopard, Ross, bearded, and ribbon seals; have long-range underwater acoustic displays (scattergun advertising) to advertise the position of males to potential mates, rival males, or both. Their acoustic repertoires tend to be larger than the first group, but smaller than the third. They have a moderate number of stereotyped signals, which are constrained by the need to ensure that their signals are received by listening to seals at a distance. Their vocalizations tend to be stereotyped narrowband pulsed sounds and frequency sweeps, with lower maximum frequencies than both the first and third

group of seals. The third group of seals, the Weddell, harp, harbour, and ringed seals, have shorter-range advertisement displays (local advertising), which are likely used for territorial proclamation, mate attraction, or both. These species tend to have broad vocal repertoires composed of varied types of sounds, from narrow to broadband types, as well as subtle variations of specific call types.

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