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Influences of Female Pupping Habitat and Maternal Care on the Vocal Repertoire Size of Male Phocid Seals

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Abstract

Phocid life history and vocal repertoire size data gathered from the literature were examined with independent contrasts analyses to assess whether there is a significant relationship between sexual selection and vocal repertoire size. Investigations showed that the degree of polygyny does not influence vocal repertoire size of males, but was strongly influenced by the strategy of maternal care adopted by females. Species where females remain with their pups while nursing ("stay-at-home mums") have males with simple crude vocal repertoires used in male-male agonistic interactions. In these species, male elephant (*Mirounga* sp.), grey (*Halichoerus grypus*), crabeater (*Lobodon carcinophagus*), and hooded (*Cystophora cristata*) seals generally have greater access to estrus females while they are still hauled out ashore. In species where females continue to go to sea while raising their pups ("working mums"), males have broader advertising vocal repertoires. The stability of the haul-out platform during breeding used by the females makes a further impact, however. Where "working-mums" breed in unstable pack ice, males have little chance of predictably locating routes used by estrus females while traveling to and from feeding grounds. These species, the leopard (*Hydrurga leptonyx*), Ross (*Ommatophoca rossii*), bearded (*Erignathus barbatus*), and ribbon (*Histriophoca fasciata*) seals, have intermediate-sized repertoires used in long-range underwater acoustic displays (scattergun advertising). The third group, the Weddell (*Leptonychotes weddellii*), harp (*Pagophilus groenlandicus*), harbour (*Phoca vitulina*), and ringed (*Pusa hispida*) seals, have the largest vocal repertoires. In these species, "working-mums" breed in stable environments, so males perform underwater acoustic advertisement displays (local advertising) in the vicinity of predictable feeding routes used by estrus females. Because these signals are not constrained by propagation, a large array of sound types have developed.

Key Words: Phocids, vocal repertoire size, maternal care, comparative analyses, pupping, habitat

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 confirmed by Thomas & Stirling (1983) who noted that gregarious polygynous species have more highly developed vocal repertoires than seals that are distributed in serially monogamous pairs or at low breeding densities. This relationship was supported by Cleator et al. (1989) who noted that the highly polygynous Weddell (*Leptonychotes weddellii*) and harp (*Pagophilus groenlandicus*) seals had larger vocal repertoires than solitary species such as the crabeater (*Lobodon carcinophagus*), Ross (*Ommatophoca rossii*), ribbon (*Histriophoca fasciata*), hooded (*Cystophora cristata*), and bearded (*Erignathus barbatus*) 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). More recent studies (Rogers, 2003; Stirling & Thomas, 2003) re-examined this relationship, focusing more broadly among the phocid seals and both studies found that the mating system or degree of polygyny did not directly influence the male vocal repertoire.

Stirling & Thomas (2003) found that the development of a diverse underwater repertoire, with geographic variation, was consistently associated with the development of genetic population structure and geographic fidelity. Rogers (2003) examined other features and found that repertoire size was influenced by the number of days males had access to estrus females; degree of sexual dimorphism in weight; stability of the haul-out platform; and the density of the colony during the breeding season. Both comparative studies did not consider phylogenetic relationship, however, which assumes that the development of repertoire size has occurred in the absence of phylogenetic inertia, which may or may not have been the case. To identify whether a correlation exists between repertoire size and life history parameters, phylogenetic inertia needs to be discounted.

In this discussion paper, the influence on the development of the vocal behaviour of male phocid seals will be examined in a fashion which accounts for phylogeny. Factors examined include (1) degree of polygyny; (2) degree of sexual dimorphism, including weight and length; (3) density during the breeding season; (4) stability of the haul-out platform during breeding; (5) duration of lactation; (6) number of days that males have no access to females; and (7) predictability of males accessing females.

Materials and Methods

Variable Definitions

Repertoire Size—The number of underwater and aerial vocalisation types produced by the males of each phocid species was taken from the literature (Table 1). Calls that have not been included are cow and pup calls; calls produced by animals of unknown sex; clicks and those produced as part of maze experiments for the grey seal (*Halichoerus grypus*) (Oliver, 1977); and ultrasonic sounds produced by leopard seals (Hydrurga leptonyx) chasing fish in the dark (Thomas et al., 1982). 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 vocalisations described for any region was 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 may reflect interindividual, 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 lumper's perspective.

Male Ability to Predict Access to Estrus Females—This was coded as 3 = low predictability—movement of cows is unpredictable both in space and time because cows pup alone in the drifting pack-ice and there is no attending male; 2 = medium predictability—cows forage throughout 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 estrus; or 1 = high predictability—cows remain with their pups until they come into estrus and there is an attending bull (Rogers, 2003; Table 2).

Duration of Lactation—The length of lactation in days is given in Table 2 and the reference for each species in this table is Rogers (2003).

Stability of Haul-Out Platform During Breeding—This was coded as 3 = pupping on pack ice, 2 = pupping on fast ice, and 1 = pupping on land (Rogers, 2003; Table 2).

Sexual Dimorphism Length and Weight—Body lengths and body weights were gathered from Bininda-Emonds & Gittleman (2000). Dimorphism was calculated as the log of male size/female size; this equals the log of male size minus the log of female size (Lindenfors et al., 2002).

Degree of Polygyny—This was coded as 4 = extreme polygyny (mating with at least 15 to 20 females), 3 = moderate polygyny, 2 = slight polygyny, and 1 = serial monogamy (Table 2).

Days Males have No Access to Hauled-Out Estrus Females—This was calculated as the number of days from parturition to estrus minus the number of days after parturition that females return to the water (Rogers, 2003; Table 2).

Density of Mothers and Pups During the Breeding Season—This was coded as 1 = widely dispersed, 2 = small groups, 3 = moderate-sized groups, and 4 = large groups (Rogers, 2003; Table 2).

Independent Contrasts Analysis

The independent contrasts method (Felsenstein, 1985) using the Phenotypic Diversity Analysis Program (PDAP) (Garland et al., 1993), specifically the independent contrasts module of PDTREE (Garland & Ives, 2000; Garland et al., 1999), was used to investigate the selection pressures behind phocid vocal repertoire development. The phylogeny used follows the phylogenetic tree for the Phocidae described by Bininda-Emonds et al. (1999). Polytomies were handled by using zero-length branches (Felsenstein, 1985). Branch lengths were set to unity for each of the response and predictor variables. These proposed branch lengths were verified empirically for each variable using graphical analysis where the standardized independent contrasts were plotted versus their standard deviations (Garland et al., 1992). There were no significant trend in the plots to indicate that the contrasts were not adequately standardized.

Table 1. The number of underwater and in-air vocalisation types produced by male phocids

Seal species	Maximum number of call types	Reference
Bearded	6	5 call types, trills from seals in Alaska (Cleator et al., 1989) 6 call types, trills in Ramsay Island (Cleator et al., 1989) 4 call types, trills in Hudson Bay (Cleator et al., 1989) 3 call types, trills in Baffin Island (Cleator et al., 1989) 2 call types, trills in Dundas Island (Cleator et al., 1989) 6 call types, trills in Table Island (Cleator et al., 1989) 3 call types, trills in the Canadian Arctic (Terhune, 1999) 4 call types, trills in Svalbard (Van Parijs et al., 2001)
Crabeater	1	1 call type, the groan (Stirling & Siniff, 1979)
Grey	4	4 call types (Asselin et al., 1993): the roar also called the male roar (Schneider, 1974), the growl also called the hum 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)
Harbour	5	5 call types in California (Hanggi & Schusterman, 1994) 1 call type in Moray Firth (Van Parijs et al., 2000) 2 call types in Orkney (Van Parijs et al., 2000)
Harp	18	16 call types from seals in Canada (Møhl et al., 1975) 18 call types Jan Mayen (Terhune, 1994) 18 call types in St. Lawrence (Perry & Terhune, 1999; Terhune, 1994) 18 call types from captive seals (Serrano, 2001)
Hooded	3	1 call type in Magdalen Islands (Terhune & Ronald, 1973) 3 call types or 'orders' of sounds (Ballard & Kovacs, 1995)
Leopard	12	4 call types in South Shetland Islands (Stirling & Siniff, 1979) 12 call types in Eastern Antarctica (Rogers et al., 1995) 5 call types at McMurdo Sound (Thomas & Golladay, 1995) 9 call types at Palmer Peninsular (Thomas & Golladay, 1995)
Northern elephant	3	3 call types (Bartholomew & Collias, 1962) 2 call types (Shipley et al., 1981) 3 call types (Shipley et al., 1986)
Ribbon	4	4 call types (Watkins & Ray, 1977)
Ringed	6	6 call types, Valaam Archipelago (Kunnasranta et al., 1996)
Ross	3	3 call types (Watkins & Ray, 1985)
Southern elephant	1	1 call type (Sanvito & Galimberti, 2000)
Weddell	34	12 in-air call types (Terhune et al., 1993) 34 underwater call types in McMurdo region (Thomas & Kuechle, 1982) 21 underwater call types Palmer Peninsula (Thomas & Stirling, 1983) 49 underwater call types, with 20 heard more than infrequently (Pahl et al., 1997)

Statistics

An analysis of the selection pressures behind phocid vocal behaviour development needs to show that variation in sexual selection characteristics (days to estrus, predictability, duration of lactation, stability of haul-out platform, sexual dimorphism length, sexual dimorphism weight, degree of polygyny, harem size, days with no access, density during breeding season, and days to foraging) are correlated to varying levels of variation in vocal repertoire size across the phocids. Multiple regression analysis with a forward-stepwise elimination process was used to ascertain if there were relationships among response variables to find the best predictors of repertoire size in male phocid vocal behavior. It does not identify any underlying causal mechanisms. 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

Two significant predictors (Multiple R = 0.965; F = 11.250; DF = 6, 5; $p = 0.009$) described the

Table 2. Variables used in multiple regression analysis against repertoire size

Seal species	Total number calls	Male ability to predict access to estrus females	Duration lactation (days)	Stability of haul-out platform during breeding	Sexual dimor-phism weight (kgs)	Sexual dimor-phism length (m)	Degree polygyny	Days males have no access to hauled-out estrus females	Density during breeding season (# / km)
Bearded	6	3	24	3	-0.02	0.00	1	23	1
Grey	3	1	18	1	0.18	0.08	3	0	3
Harbour	5	2	24	1	0.08	0.02	2	12	3
Hooded	3	1	4	3	0.19	0.10	1	0	1
Ribbon	4	3	25	3	0.07	0.00	1	5	1
Harp	18	2	12	3	0.02	0.02	2	9	3
Ringed	6	2	42	2	0.03	0.00	1	10	1
Northern Elephant	3	1	27	1	0.65	0.18	4	0	4
Southern Elephant	1	1	23	1	0.84	0.24	4	0	4
Leopard	12	3	30	3	-0.05	-0.05	1	28	1
Weddell	34	2	49	2	-0.02	-0.02	3	27	3
Ross	3	3	28	3	-0.03	-0.03	1	27	1
Crabeater	1	1	28	3	-0.01	0.00	1	0	1

repertoire size of male phocid seals via a stepwise regression: stability of the haul-out platform during breeding (beta = 0.996) and the days males have no access to hauled-out estrus females (beta = 0.750). Four other predictor variables—density during breeding season (beta = 0.607), duration of lactation (beta = 0.294), the males' ability to predictably access estrus females (beta = -0.57), and the degree of polygyny (beta = 0.627)—although not significant, were used in the model. The two remaining variables—sexual dimorphism length and sexual dimorphism weight—were eliminated from the model. Therefore, species where the males do not have access to estrus females for long periods and breed in stable environments tend to have more calls in their repertoires; whereas species have reduced repertoires where males have greater access to estrus females while they are still hauled out and/or where females breed on unstable platforms.

Discussion

This paper is a starting point to commence discussion about the development of phocid vocal behaviour as it coincides with the time when our knowledge of phocid life history strategies and vocal behaviour is coming to light. The conclusions drawn here must be considered with caution, however, as there are still gaps in our knowledge for many of the phocid species, and many previously thought ideas have been recently overturned. So, with further information, some species may move into different categories from those in which they have been considered here.

Male vocal repertoire size appears to have been influenced by the number of days that males did not have access to hauled-out estrus females and the stability of the haul-out platform during breeding. Both these features were reported as important positive predictors of vocal repertoire in a previous comparative study (Rogers, 2003). That same study reported that sexual dimorphism in weight and densities during the breeding season also were important predictors which were not found here. Phylogenetic relationships were not considered in the previous study and so the development of repertoire size was assumed to have occurred in the absence of phylogenetic inertia; however, my results suggest that this has not been the case. The data used by Rogers (2003) were assumed to be independent of one another, whereas, in reality, the phocid seals are part of a hierarchically structured phylogeny so the data should not have been regarded as being independent (Felsenstein, 1985; Harvey & Pagel, 1991). This may have led to the statistical overstating of the significance of sexual dimorphism and density in influencing repertoire size.

Number of Days that Males Do Not Have Access to Hauled-Out Estrus Females

The maternal strategy used by females to look after their pups not only influences the males' ability to access mates, but also their vocal repertoire size. The longer males can guard estrus females while hauled out ashore the more simple the male's vocal repertoire, whereas species with broad complex vocal repertoires typically had males with limited access to estrus females. Male phocids wait for females to come into estrus, which is around the time that their pups are weaned. Depending on the species, mating occurs either on land, as in the northern and southern elephant seals (Hindell, 2002); on ice, as in the crabeater seal (Bengtson, 2002); in the water in the bearded (Kovacs, 2002a), harbour (Burns, 2002), ribbon (Fedoseev, 2002), harp (Lavigne, 2002), ringed (Miyazaki, 2002), leopard (Rogers, 2002), Weddell (Thomas, 2002a), and Ross (Thomas, 2002b) seals; or both in water and on land in the grey seal (Hall, 2002); or in water and on ice for the hooded seal (Kovacs, 2002b). If mating is on land or ice, males can use force to coerce females to mate; whereas if they mate in the water, this is no longer possible because females are more mobile in this three-dimensional environment. If a female goes to sea prior to coming into estrus, males can no longer physically overpower them to ensure mating and this directly impacts their ability to access estrus females.

Species where females continue to return to sea while nursing their pups, either to hunt or avoid predators, are referred to here as "working mums." Cows leave their haul-out site either taking their pups or leaving them alone, travel out to sea, and return later to the haul-out site to rest and nurse their pups. In "working-mum" species, cows may return to sea at various times prior to weaning; some go to sea through most of the nursing period such as the bearded (Kovacs, 2002a) and Weddell (Thomas, 2002a) seals, while others just prior to weaning such as the harbour (Burns, 2002), harp (Lavigne, 2002), ribbon (Fedoseev, 2002), and ringed (Miyazaki, 2002) seals. If a female returns to the water prior to coming into estrus, males have little opportunity to forcibly coerce them to mate, and an aquatic female is highly mobile, so males have little chance of guarding these pre-estrus females. In "working-mum" species, males need to convince free-moving aquatic females to mate if they are to be successful. Males need to advertise their presence to females through underwater vocalisations. The number of days that a male does not have access to estrus females is dependent on the time period prior to estrus that a female returns to sea. The longer the time period prior to estrus that males could not access hauled-out females, the more likely it was that males had a large complex vocal repertoire.

This is different than in other phocid species, such as the grey (Hall, 2002), hooded (Kovacs, 2002b), crabeater (Bengtson, 2002), and northern and southern elephant (Hindell, 2002) seals where females remain with their pups during the entire lactation period, leaving the haul-out site only when pups have weaned; these seals are referred to here as "stay-at-home mums." Males are guaranteed mating opportunities by guarding positions favored by females (resource guarding) or guarding females themselves directly (mate guarding) until they come into estrus near the end of weaning. Males maintain strategic positions through direct physical contests, and as the breeding success of a male is linked with guarding prime positions from other males, intrasexual competition is high. Mating occurs on land, on ice, or at the water's edge as the females leave the haul-out site. Males use force to coerce females to mate and tend to be larger than the females in the grey (Hall, 2002), hooded (Kovacs, 2002b), and northern and southern elephant seals (Hindell, 2002). Perhaps the males of "stay-at-home-mum" species tend to have simple limited vocal repertoires because males do not need to convince females to mate, using forceful coercion instead. Their communication is directed predominantly towards other males through intrasexual competitive displays.

Stability of the Haul-Out Platform During Breeding

The second predictive factor was the stability of the haul-out platform used by the females to raise their pups. Phocid seals breeding in unstable habitats tend to have reduced vocal repertoires compared to those breeding in more stable environments, such as on land or on fast ice. Seals pupping on the unstable pack ice, such as the bearded (Kovacs, 2002a), hooded (Kovacs, 2002b), ribbon (Fedoseev, 2002), harp (Lavigne, 2002), leopard (Rogers, 2002), Ross (Thomas, 2002b), and crabeater (Bengtson, 2002) seals, are faced with enormous constraints. Throughout the breeding season, pack ice begins to disintegrate in sea swells as they deteriorate in the warmer spring/summer weather. Females raise their pups quickly before their pupping platforms disappear. The hooded seal has an average four-day lactation length (Kovacs, 2002b), which highlights the remarkably short lactation periods of some pack ice species. Pack-ice seals tend to be solitary and widely dispersed, and females are likely to be in estrus for only short periods of time. In the "stay-at-home-mum" pack ice breeders, such as the hooded (Kovacs, 2002b) and crabeater (Bengtson, 2002) seals, females have accompanying males guarding them until they come into estrus so that a single floe will house a triad of a cow, pup, and bull (Bengtson, 2002); whereas in the "working-mum" pack ice breeders, such as the leopard (Rogers, 2002), Ross (Thomas, 2002b), bearded (Kovacs, 2002a), and ribbon (Fedoseev, 2002) seals, there are no accompanying males and widely dispersed lone cow-pup pairs are common. Pups of some of the "working-mum" species, such as the bearded seal (Kovacs, 2002a), are able to swim soon after birth so that pups can move from floe to floe with their mothers. Ice floes move with the whim of winds and currents so "working-mum" females may never return to the same site. Males have little chance of predicting the movements of females in the "working-mum" pack-ice breeders, so they would need to advertise broadly to find estrus females within the widely dispersed population. The pack ice is a noisy environment, however, so transmitting a signal which is clear and audible over long distances brings propagation challenges. Having many subtly different calls may make it confusing for a seal listening at a distance. Fewer styled calls repeated over long periods may ensure that the signal gets through. "Working-mum" species pupping on stable land or fast-ice environments are not faced with these same constraints.

"Working-mum" females breeding in stable environments are less concerned that their pupping habitat will break up and so tend to have longer duration lactation periods such as 28 days in the harbour seal (Burns, 2002), 42 in the ringed seal (Miyazaki, 2002), and 45 in the Weddell seal (Thomas, 2002a). In addition, they can leave their pups in the same area, so they will travel along predictable routes while moving between foraging grounds and the breeding haul-out sites. Males can predict where females will travel and position themselves along these routes to advertise vocally under water to the females as they travel back and forth. Because males know where to find estrus females, their advertising displays do not need to travel great distances. The signals of species advertising to a local audience are less 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.

In conclusion, there appears to be three groups of vocal repertoire strategies among the male phocid seals. In the first group, the elephant (*Mirounga* sp.), grey, crabeater, and hooded seals, males have smaller more simple repertoires. This group represents species where males have a high level of predictability of finding, guarding, and then mating an estrus female. Females are "stay-at-home mums," remaining hauled-out ashore with their pups until weaning. The timing of weaning coincides roughly with when the cows come into estrus so that attending males have greater access to estrus females. Males need to secure a position where they can monopolize females until mating either by guarding a territory, guarding a harem of females, or escorting a single, pre-estrus female. There is a great deal of aggression between males for positions which will lead to mating. Degree of polygyny and density of the breeding colony are unimportant, and the two extremes of this are represented in this group. Elephant seals are highly polygynous and breed in dense colonies of many thousands of seals (Hindell, 2002) compared with pack-ice breeders—the crabeater (Bengtson, 2002) and hooded (Kovacs, 2002b) seals—which are monogamous and breed at low densities. The vocal displays of seals in this group appear to be agonistic in character and associated with aggressive encounters between males.

The males of the second group of phocid seals, the leopard, Ross, bearded, and ribbon seals, have an intermediate-sized vocal repertoire. Cows are likely to be "working-mums," returning to sea prior to estrus. They breed in the highly unstable pack ice and are solitary and widely spaced. Females are in estrus for only a short period of time. Males have little chance of guarding or predicting the movements of aquatic pre-estrus females, so they advertise broadly to find females within the widely dispersed population. Having an intermediate number of calls repeated over long periods would ensure that the males' signal is broadcast widely to a scattered audience (scattergun advertising).

Males of the third group of seals, the Weddell, harp, harbour, and ringed seals, tend to have the larger complex vocal repertoires. The females of this group, although "working-mums," are highly predictable in their aquatic movements. Because males know where to find estrus females, their underwater advertising displays do not need to travel great distances (local advertising). This means that their displays are not constrained by propagation needs. These seals tend to have a larger vocal repertoire composed of many complex and subtle variations.

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