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Changes in the distribution and activity of female harbour seals during the breeding season: implications for their lactation strategy and mating patterns

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Summary

1. Adult female harbour seals from NE Scotland were radio-tracked to follow changes in their distribution and activity during the breeding season.
2. Seals foraged up to 45 km from haul-out sites, but females with pups restricted their range markedly during the early part of the lactation period. However, foraging trips resumed before the expected weaning date, indicating that female harbour seals do not fast throughout lactation.
3. The duration of the period that females spent inshore with young pups was positively related to female body size, suggesting that the species' small size may demand that they feed to maintain lactation.
4. Foraging in late lactation results in females becoming highly dispersed during the mating period and it is clearly uneconomic for males to monopolize females.

Key-words: body-size relationships, fasting, foraging behaviour, *Phoca vitulina*, spatial distribution.

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Introduction

Studies of pinniped reproductive strategies have concentrated on those species which mate on land. These are primarily otariids, but include a few phocids such as elephant seals, *Mirounga leonina* and *M. angustirostris* (Le Boeuf 1974; McCann 1981) and land-breeding grey seals, *Halichoerus grypus*, (Anderson, Burton & Summers 1975) which fast throughout the lactation period. In contrast, most phocids spend part of the lactation period in the water, during which time they may feed (Andersen & Fedak 1987). These species also tend to form more dispersed breeding groups, particularly on ice (e.g. Crabeater seals, *Lobodon carcinophagus*) and several species appear to mate in the water [e.g. Weddell seals, *Leptonychotes weddelli* (Cline, Siniff & Erickson 1971)]. The resulting differences in female dispersion would be expected to result in a wider range of mating patterns than those seen amongst land-breeding pinnipeds (Stirling 1975; Boness 1991; Le Beouf 1991), but few data exist to examine this hypothesis.

Female harbour seals (*Phoca vitulina*) give birth on land, but spend much of the lactation period in the water with their pups. During this time they may feed (Costa 1991), but the extent to which foraging is constrained by lactation remains unknown. Terrestrial matings are seen only rarely (Boulva & McLaren 1979; Allen 1985) and most attempts by males to mate on land are rebuffed (Bishop 1968; Godsell 1988; Thompson 1988). Consequently, it is generally accepted that copulation occurs in the water. A variety of different breeding habitats are used by harbour seals including ice, rocky shores and inter-tidal sandbanks (Bigg 1981) and breeding groups range in size from one or two to many hundreds of adult females. These intra-specific differences in female dispersion make harbour seals an ideal subject for an assessment of the effect of density and spacing pattern on pinniped mating strategies. However, the problems involved in studying the species' aquatic behaviour have resulted in only limited information on both their lactation and mating patterns.

Nevertheless, it is now clear that early suggestions that harbour seals were monogamous or promiscuous (e.g. Bartholemew 1970) were based more on a lack of data than any real perception of the species mating system. In particular, these studies were constrained by the belief that polygyny could develop only on land, where males could defend and dominate harems of females (e.g. Bartholemew 1970). More recent studies indicate that harbour seals are

likely to be polygynous given the observed dergee of sexual dimorphism (Boulva & McLaren 1979; Härkönen & Heide-Jørgensen 1990) and male–male competition (Bishop 1968; Sullivan 1981; Slater & Markowitz 1983; Thompson 1988). However, the mechanisms by which males might obtain multiple matings remain unclear, especially because little is known of the aquatic distribution of females.

In this paper, we describe how the terrestrial and aquatic distribution of female harbour seals changes during the breeding season. We aimed, first, to determine the extent to which lactation constrained female foraging activity, and secondly, to describe the distribution of females during the mating period. We then explore the implications of these results for the species lactation and mating strategies.

Methods

This study was carried out in the inner Moray Firth, Scotland (57°41'N, 4°W) during the summers of 1988, 1989 and 1991. In this area, common seals haul-out on inter-tidal sandbanks throughout the year. During the summer breeding season, females with pups occur at sites in the Beauly, Cromarty and Dornoch Firths (Fig. 1.). At these sites the first births occur in early June and peak numbers of pups are seen in the last week of June and first week of July (P.M. Thompson, Unpublished data).

Spatial and temporal changes in the distribution of females were assessed using VHF radiotelemetry. Seals were captured at haul-out sites during May; in the Inverness Firth in 1988 and in the Dornoch Firth in 1989 and 1991. Once secure in hand nets they were sedated (Thompson *et al.* 1992), and weights and standard measurements were taken. A 200-g radio-tag was then glued to the hair on top of the head (Fedak, Anderson & Curry 1983) and a large fluorescent mark painted on the back for visual identification (Thompson 1989).

Radio-locations were obtained by triangulation using hand-held directional aerials from coastal hill-tops, and were accurate to ±7.5° (Thompson & Miller 1990). In 1988, locations were determined each day at random times. In 1989 and 1991 seals were located once a day, at standardized times, for 6 days each week. Estimates of range size were calculated using the MCPAAL package (National Zoological Park, Smithsonian Institute, Washington, USA). Changes in range size over the season were assessed by calculating the 7-day minimum convex polygon range size for each date, using the location for that date and the 3 days on either side of it. No account was taken of the possible error in locations in calculating range size.

Activity patterns were monitored using permanent recording stations (Nicholas, Fedak & Hammond 1992) which recorded whether radio-tagged seals were diving, hauled-out or absent from inshore haul-out areas (Thompson *et al.* 1989,; Thompson & Miller 1990). The distribution of the mid-points of haul-out bouts were assessed in relation to tidal and diurnal cycles (Thompson & Miller 1990) using Watson's *U* test (Batschelet 1981).

Each year, recording stations were located to ensure coverage of the haul-out sites used by radio-tagged seals. The location and, thus, the exact range of recording stations varied between sites and

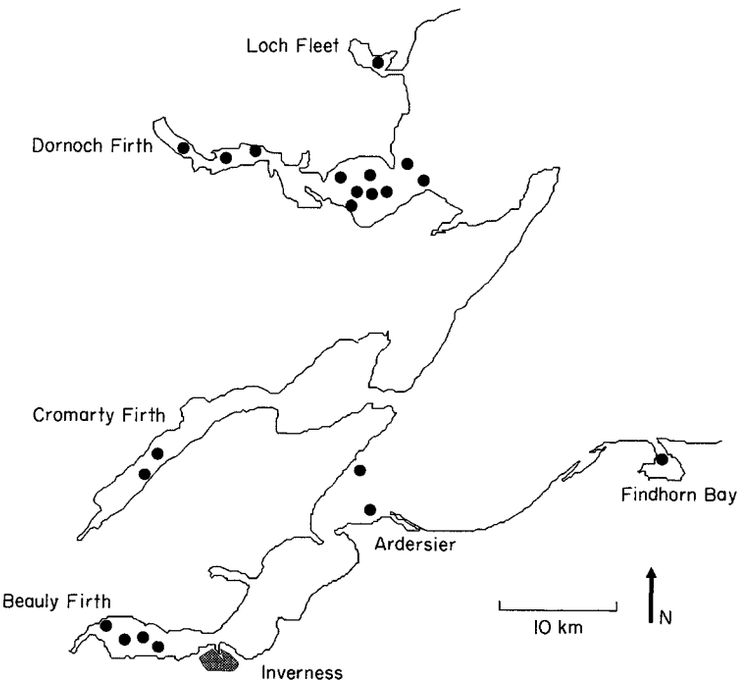

Fig. 1. A map of the study area showing the position of harbour seal haul-out sites.

between years. Consequently, information on the absence of seals from inshore haul-out areas was based primarily on daily radio-locations. Data from recording stations were then used to confirm whether or not seals had returned to haul out between daily locations.

When radio-tagged females were located at haul-out sites, attempts were made to observe these seals directly and determine whether their pups were present. This was often impossible in 1989 and 1991 because most haul-out sites in the Dornoch Firth were >1 km from the shore. However, aerial surveys were made on 23 and 29 June, and 3 July 1989 to confirm the presence of pups.

Results

HAUL-OUT DISTRIBUTION AND BEHAVIOUR

Eight adult females were radio-tracked during the period of study. Of these, one was captured in the Inverness Firth in 1988 and the remainder were caught in the Dornoch Firth; six in 1989 and one in 1991. All females used more than one haul-out site. However, in most cases females used alternative sites within a few kilometres of each other, in the same inner firth. The exception was female 8, who used a haul-out site on the open coast 15 km north-east of Loch Fleet (Fig. 1). This site was outwith the area covered by the permanent recording stations and records of her haul-out activity, therefore, relate only to her activity in the inner firth.

The haul-out patterns of all females were dominated by the tidal cycle, although the time of day also had a significant, though smaller, effect on the behaviour of one seal (Table 1).

Table 1. Analysis of the effects of (a) diel and (b) tidal cycles on the timing of haul-out bouts for the seven females which had pups. n is the number of haul-out bouts. Mean times for the mid-points of haul-out bouts are presented where Watson's *U* statistic indicates that the timing of bouts differed from random. *r* is a measure of the strength of any relationship with tidal or diel cycles. For tidal state, 0/360° = high tide and 180° = approximate low tide

(a) Time of day

Seal	*n*	Mean time of mid-point of haul-out bout	*r*	*U*	*p*
F1	99	–	–	0·12	NS
F4	107	–	–	0·06	NS
F5	101	02:15	0·15	0·19	<0·05
F6	88	–	–	0·07	NS
F8	57	–	–	0·11	NS
F9	75	–	–	0·08	NS
F15	104	–	–	0·14	NS

(b) Tidal state

Seal	*n*	Mean tidal state in middle of haul-out bout	*r*	*U*	*p*
F1	99	183·6°	0·61	2·24	<0·01
F4	107	181·0°	0·87	4·85	<0·01
F5	101	199·6°	0·67	2·69	<0·01
F6	88	179·6°	0·73	2·56	<0·01
F8	57	189·8°	0·68	1·49	<0·01
F9	75	182·6°	0·91	3·02	<0·01
F15	104	158·0°	0·50	1·47	<0·01

FORAGING BEHAVIOUR AND DISTRIBUTION

All females spent part of their time outside the inner firths (Fig. 2), travelling between 29 and 46 km to their foraging areas (Table 2). Individual females returned to apparently favoured foraging areas, but there was considerable overlap among the areas used by seals from the Dornoch Firth (Fig. 2). The duration of foraging trips varied from a few hours to 6 days, but trips of 2 days or more were recorded for all females (Table 2).

CHANGES IN BEHAVIOUR WHILE WITH PUPS

Six females were seen closely associated with a pup on at least one occasion during the study (Table 2). All six of these showed similar changes in behaviour over the course of the breeding season (Fig. 3). In the pre-pupping period, they made regular trips

Table 2. Information on the standard length (nose–tail), reproductive success and foraging trip characteristics of eight adult female harbour seals radio-tracked during the breeding season.

Female number	Length (cm)	Whether or not seen with pup	Max. foraging trip duration (hours)	Max. distance from haul-out site while on foraging trip (km)
F1	145	Yes	158·2	46
F4	138	Yes	137·5	29
F5	142	Yes	99·8	33
F6	134	Yes	97·9	31
F7	129	No	43·5	27
F8	135	Yes	98·3	46
F9	136	Yes	131·4	31
F15	141	No	154·0	32

between haul-out and foraging areas. Around the time of pupping, these trips ceased and females were located within 2 km of haul-out sites each day, while data from recording stations indicated that females usually hauled out on every low tide. After a period of between 10 and 24 days, movements away from haul-out areas resumed. No similar restriction in foraging range was seen for the 1989 female which was not seen with a pup (Fig. 3: F7). The female followed in 1991 (F15) was not observed again after capture. However, her behaviour was similar to that of the six females which were known to have had pups (Fig. 3) and it is assumed that she too gave birth during the period of study.

These changes in the behaviour of females with pups resulted in an overall reduction in mean range sizes during the middle of the summer (Fig. 4), when females were concentrated in inshore haul-out areas. The number of hours hauled-out each day also increased in mid-summer, resulting in a significant negative correlation between range size and daily haul-out period (Fig. 5).

The haul-out sites used by most females also changed during the summer. During the early part of the lactation period alternative sites were within 1–3 km of each other. However, five of the females with pups switched to more distant sites at the time that they resumed foraging trips. These new sites

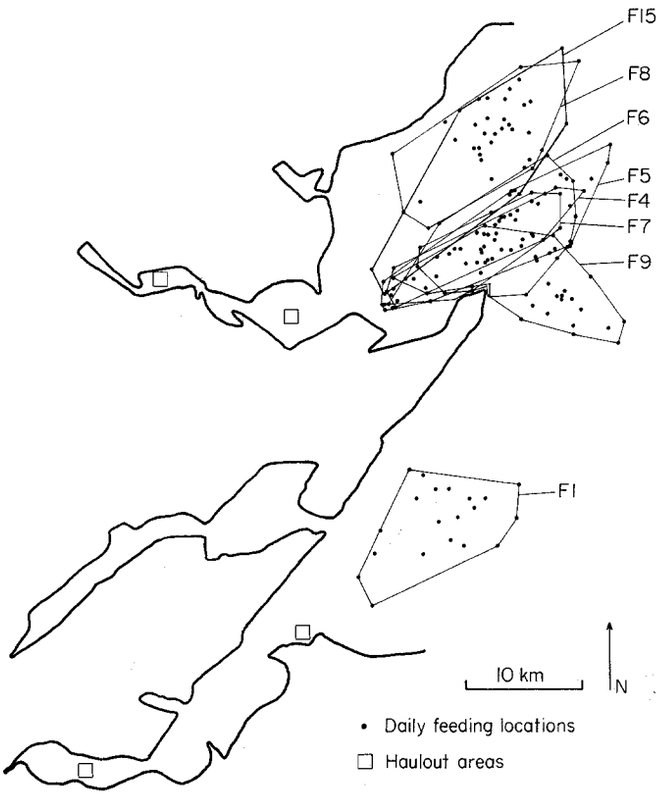

Fig. 2. Feeding locations of eight adult female harbour seals, with minimum convex polygons surrounding the locations for each individual. All locations <2 km from a haul-out site have been ommitted.

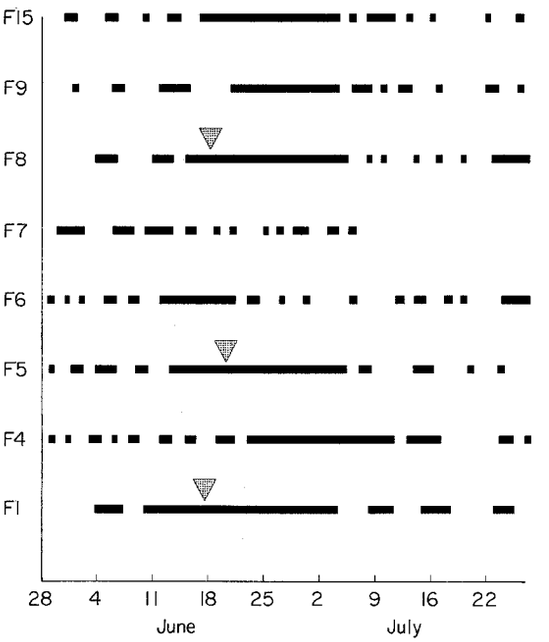

Fig. 3. Presence of radio-tagged females (solid bars) in the inshore haul-out areas, with approximate date of pupping (▽) where known.

were at the entrance to the firths and closer to feeding areas, but were not generally used by mothers with young pups. Three of these females moved only 3–6 km, but F1 and F8 travelled 22 and 30 km. These two females continued to use these sites for the next 20 and 10 days, respectively, having moved to them when their pups were only 15–17 days old.

Although all females with pups showed a restriction in range around the time of pupping, the duration of the period spent in the haul-out areas varied from 10 to 24 days (Fig. 3). The length of this period was significantly correlated with female body size (Fig. 6); larger females remained in the haul-out areas longer than smaller females before resuming foraging. Because of the difficulty of direct observations at these sites, it was not possible to determine exact parturition dates. However, regular sightings of three females showed that the restriction in range did not coincide exactly with the time of birth. In these cases, females stopped making foraging trips at least 2, 5 and 6 days before giving birth (Fig. 3).

Discussion

FEMALE LACTATION STRATEGIES

The use of foraging grounds outside the inner firths confirms earlier findings (Thompson & Miller 1990) that harbour seals in this area regularly move up to 50 km from their haul-out sites. These movements are likely to be associated with feeding although this has yet to be confirmed. Similarly, as seen in studies from other areas (Pitcher & McAllister 1981; Yochem *et al.* 1987; Thompson *et al.* 1989), seals

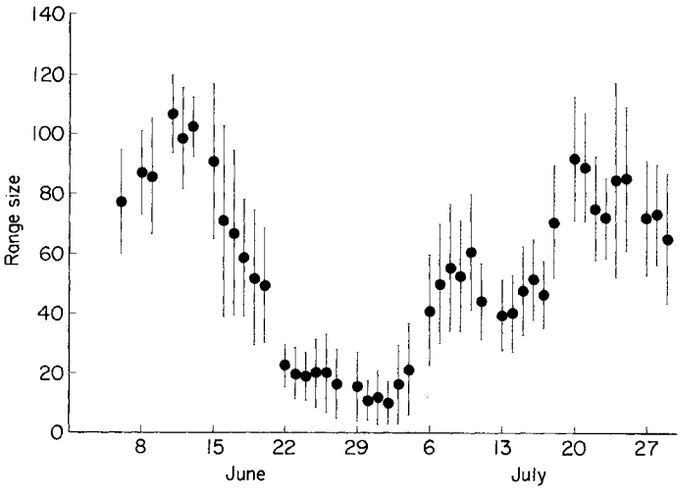

Fig. 4. Changes in mean (±1 standard error) minimum convex polygon 7-day range sizes for females with pups. The mean for each day includes data from the 3 days either side. Consecutive points are, therefore, not independent.

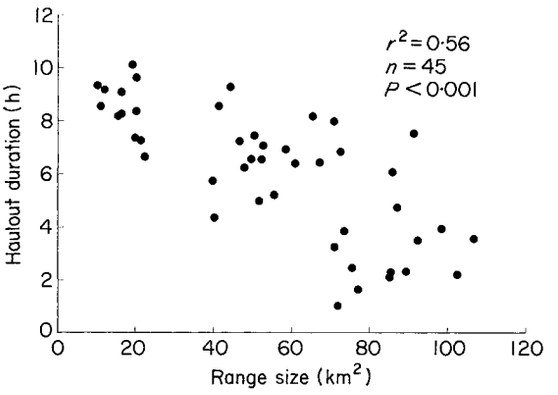

Fig. 5. Relationship between mean range size and mean number of hours hauled out each day, for all females with pups.

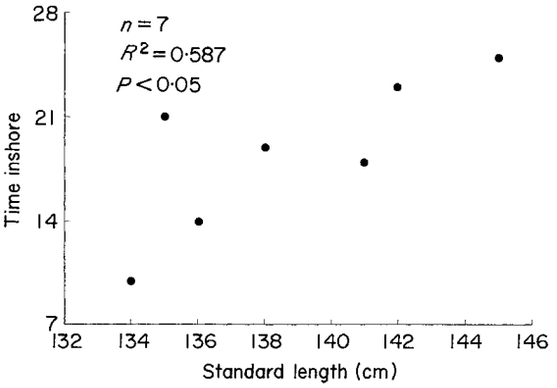

Fig.6. Relationship between the duration of the period spent inshore with pups (days) and female standard length (cm).

did not come ashore to haul-out on a daily basis throughout most of the study period. However, females did restrict their range considerably during the pupping period and also increased the amount of time that they spent on land. Although some opportunistic feeding may have continued in the waters around the haul-out sites, these data suggest that female movement, and probably foraging activity, is constrained when they are with young pups. We were unable to determine exactly how long the females in this study remained with pups, but longitudinal studies of marked animals from other populations indicate that lactation lasts between 24 (Bowen 1991) and 31 (Allen 1988) days. In our study, females remained in the haul-out areas for between 10 and 24 days, with parturition occurring 2–6 days from the start of this period. It therefore appears that, although females feed little in the early part of lactation, their foraging trips resume before the pups are weaned. This conclusion is supported by studies of inshore activity patterns of harbour seals from other populations (Allen 1988; Thompson *et al.* 1989; D.J. Boness, personal communication). No data were available on feeding locations in these studies, but radio-tagged females did remain close to haul-out sites for around 2 weeks after pupping before spending increasing amounts of time away at sea.

Our results also suggest that the extent of feeding activity during lactation is related to female body size, with large females remaining inshore for longer before resuming foraging. Larger females should be able to fast for longer because a female's metabolic overhead (Fedak & Anderson 1987) increases with body size at a lower rate than the amount of energy that can be stored as blubber (Costa 1991). Within-population differences in fasting ability could, therefore, result from age or heritable differences in body size, while geographical variation in body size (Härkönen & Heide-Jørgensen 1990) could result in between population differences in the extent of feeding during lactation.

It is not known whether pups remained with females while they were on feeding trips during late

lactation. In five cases, however, females switched to a different haul-out site at the time that foraging resumed. Assuming that weaning occurred at the time we suggest, pups must have travelled distances of up to 30 km with their mothers to alternative haul-out sites. Allen (1988) confirmed that females continued to feed their pups after the onset of foraging trips, but could not determine whether pups remained with females while foraging. On Sable Island, marked females were observed alone in the water and were later seen with their pups (Godsell 1988), but this site differs from those in this study and that of Allen (1988) because land surface remains available throughout the tidal cycle on Sable Island.

It has been suggested that the three pinniped families each have a distinct lactation strategy (Anderson & Fedak 1987; Oftedal *et al.* 1987). Thus, the Phocidae accumulate reserves prior to parturition in preparation for a brief lactation period, during which they fast while the Otariidae alternate nursing periods and foraging trips over an extended lactation. The Obodenidae also have an extended lactation, but the pup accompanies the female to sea, thus allowing concurrent feeding and suckling. The feeding trips which we observed during late lactation show that harbour seals have a lactation strategy which has characteristics of both the phocid and the otariid postulated patterns. The possibility also remains that, like walruses (*Odobenus rosmarus*), harbour seal pups may feed with their mothers, albeit for a much shorter period. The relationship between female body size and feeding activity indicates that this species' relatively small size may prevent it from carrying sufficient reserves to fast throughout lactation. Fedak & Anderson (1987) have suggested that the smallest phocids such as the ringed seal (*Phoca hispida*) and the Baikal seal (*Phoca sibirica*) must feed during lactation in order to maintain their long lactation periods of 40–50 days. Lactating females of several larger phocids, such as Weddell seal and ribbon seal (*Phoca fasciata*) have also been shown to feed to some extent (Burns 1981; Testa, Hill & Siniff 1989) and it now appears that phocids display a wider range of lactation strategies than studies of the more accessible species first indicated.

IMPLICATIONS FOR MATING PATTERNS

Female harbour seals come into oestrus around the time of weaning (Fisher 1954; Harrison 1960; Reijnders 1990). At this time, the females that we studied had resumed their foraging trips and were not restricted to inshore haul-out areas. Receptive females were therefore extremely dispersed and it is clear that they could not be economically monopolized by males. Consequently, the type of mating pattern to be expected for this and other aquatically mating species is likely to be constrained to a form such as serial female-defence or lekking-type polygyny (Boness 1991; Le Boeuf 1991).

Furthermore, although females returned regularly to haul-out sites during the mating period, most mothers had moved to alternative sites during late lactation. These data indicate that further studies of male display activity (Sullivan 1981; Godsell 1988) and mating (Allen 1985) should not necessarily concentrate on areas around those haul-out sites associated with pupping. Instead, males may maximize their contact with oestrus females by remaining around sites close to feeding areas or on the transit routes between feeding and haul-out sites.

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