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Distribution and activity of male harbour seals during the mating season

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Abstract. Little is known about male reproductive strategies in aquatically mating pinnipeds. To study the mating patterns of harbour seals, *Phoca vitulina*, VHF telemetry was used to relate the distribution and behaviour of adult males to the distribution of females during the summer pupping and mating season. Prior to July males occupied large and variable ranges. At the beginning of July, males decreased their mean range size, but continued to spend much of their time in the water where they made characteristic short dives. Acoustic recordings in the presence of several radiotagged males suggested that these short dives were associated with underwater vocal displays. Throughout July, males varied in the geographical areas which they used to perform these displays. Some individuals were found in the water around haul-out sites; others were located on foraging grounds, up to 50 km from pupping sites, and some were consistently located displaying on transit routes between these two areas. This study supports previous suggestions that vocalizations and diving displays may be associated with male mating behaviour, but suggests that males may display over a much wider geographical area than was previously recognized. This system of dispersed but small display territories is suggestive of lekking. However, further research on the distribution of the clumping of displaying males is required to confirm this.

Where males provide no parental care, female reproductive success is generally limited by access to resources (Emlen & Oring 1977). In contrast, male reproductive success is limited by access to females (Davies 1991). As a result, observations of male behaviour and distribution in relation to the distribution of females often provide a useful insight into a population's mating patterns.

Female phocid seals spend much of their time foraging at sea, but must return to land or ice to give birth and suckle their pups. Females can therefore show extremes of distribution patterns not seen in most terrestrial mammals. When at sea, they occur in large overlapping ranges and when on land, they can be either highly concentrated (e.g. Northern elephant seal, *Mirounga angustirostris*, Haley et al. 1994) or more widely dispersed, as is often the case on ice (e.g. the hooded seal, *Crystophora cristata*, Kovacs 1990).

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Most studies of phocid mating patterns have focused on those species that remain ashore during the mating period. In these species, such as the Northern elephant seal (Deutsch et al. 1989) and the land-breeding grey seal, *Halichoerus grypus* (Anderson et al. 1975), females are highly clumped in both space and time. As a result there can be extreme potential for polygyny, and males that defend harems (Haley et al. 1994) or successfully compete for a place within female breeding groups (Twiss et al. 1994) can attain high levels of reproductive success (Le Boeuf & Reiter 1988).

However, 15 out of the 18 phocid species mate aquatically and little is known about their male reproductive strategies. In contrast to land breeding species, females may be widely dispersed during oestrus, and theoretical expectations (Boness 1991) as well as limited empirical evidence suggest that quite different male reproductive tactics might be used. In Weddell seals, *Leptonychotes weddellii*, males appear to use visual and acoustic displays to maintain three-dimensional underwater 'territories' around breathing holes (Bartsh et al. 1992). Several other Arctic species such as

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bearded seals, *Erignathus barbatus*, harp seals, *Phoca groenlandica*, ringed seals, *Phoca hispida*, leopard seals, *Hydrurga leptonyx*, and crabeater seals, *Lobodon carcinophagus*, also have complex underwater vocalizations, but their role in mating behaviour remains unclear (Stirling 1973; Stirling & Siniff 1978; Watkins & Schevill 1979; Cleator & Stirling 1990).

Harbour seals provide an ideal species for comparative studies of the influence of environment and female distribution on phocid mating patterns (Le Boeuf 1991; Boness 1991; Thompson et al. 1994). They are the most widely distributed of pinnipeds, occur in breeding groups of one or two up to several hundred females, and can be found breeding on a variety of habitats including ice, inter-tidal sand bars and rocky beaches (Bigg 1981).

Recent evidence suggests that harbour seal females forage during late lactation (Bowen et al. 1992; Boness et al. 1994; Thompson et al. 1994). They are therefore widely dispersed during the mating season, and it is thought unlikely that it is economic for them to be monopolized by males. Nevertheless, although harbour seals offer unique opportunities for studying intraspecific variations in phocid mating patterns, empirical data on male reproductive strategies have proved difficult to obtain. Terrestrial mating is seen only rarely in this species and most attempts by males to copulate on land are rebuffed (Allen 1985; Thompson 1988). Therefore, while it is generally accepted that mating occurs in the water (Sullivan 1981) the only direct reports of aquatic mating (Venables & Venables 1957) are now believed to represent observations of sexual play by juveniles outside the normal mating period (Thompson 1988). Nevertheless, observations of aquatic displays (Sullivan 1981; Perry 1993), vocalizations (Hanggi & Schusterman 1994; Bjørge et al. 1995; D. Thompson, unpublished data), and increases in the prevalence of neck wounds on males (Thompson 1988) during the mating season, suggest that some form of male dominance system, possibly resembling a lek may be occurring (Perry 1993; Hanggi & Schusterman 1994).

Previous studies in the Moray Firth have described changes in the distribution of female harbour seals during the summer pupping, lactation and oestrous period (Thompson et al. 1994). Our aim in this study was to determine how adult male distribution and behaviour varied in relation to female distribution.

METHODS

The study was undertaken in the inner Moray Firth, Scotland (57°41′N, 4°W) during the summers of 1988, 1991, 1993, 1994 and 1995. At this time of year, both males and females haul out at sites in the Beauly, Cromarty, Dornoch and Inverness Firths (Fig. 1). Females give birth to pups between early June and the first week of July in all but the last of these areas.

Male Distribution and Dive Behaviour

We captured 20 males at haul-out sites before the pupping seasons of 1988, 1991, 1994 and 1995, in the Beauly, Dornoch and Inverness Firths. Once secure in hand nets, the seals were weighed and then sedated to minimize stress and possible stress-related mortality during handling (Thompson et al. 1992). A 200 g (0.22–0.24% of total body weight) or 80 g (0.06–0.09% of total body weight) VHF radiotag was then glued to the top of the head (Fedak et al. 1983). A 200 g (0.17–0.23% of total body weight) time depth recorder (TDR) was also glued to the back of three seals. These transmitters were well below the maximum 5% of body weight recommended for radiotelemetry studies (Cuthill 1991). The design and positioning of tags were also chosen to minimize cross-sectional area and thus decrease drag effects whilst diving (Wilson et al. 1986). Earlier observational studies involving slightly larger tags recorded no observable effects on the behaviour of instrumented seals at haul-out sites (Thompson et al. 1989).

Studies of mass change in male harbour seals from eastern Canada suggest that only males weighing more than 80 kg are reproductively active (Walker & Bowen 1993). Our sample of males could be divided into two classes based on weight. Smaller seals between 45 and 60 kg were classed as subadults and those larger animals between 80 and 126 kg were considered adult. The analyses in this paper concern the 10 individuals that weighed more than 80 kg when captured in May, and whose VHF tags did not fail or fall off before 15 July.

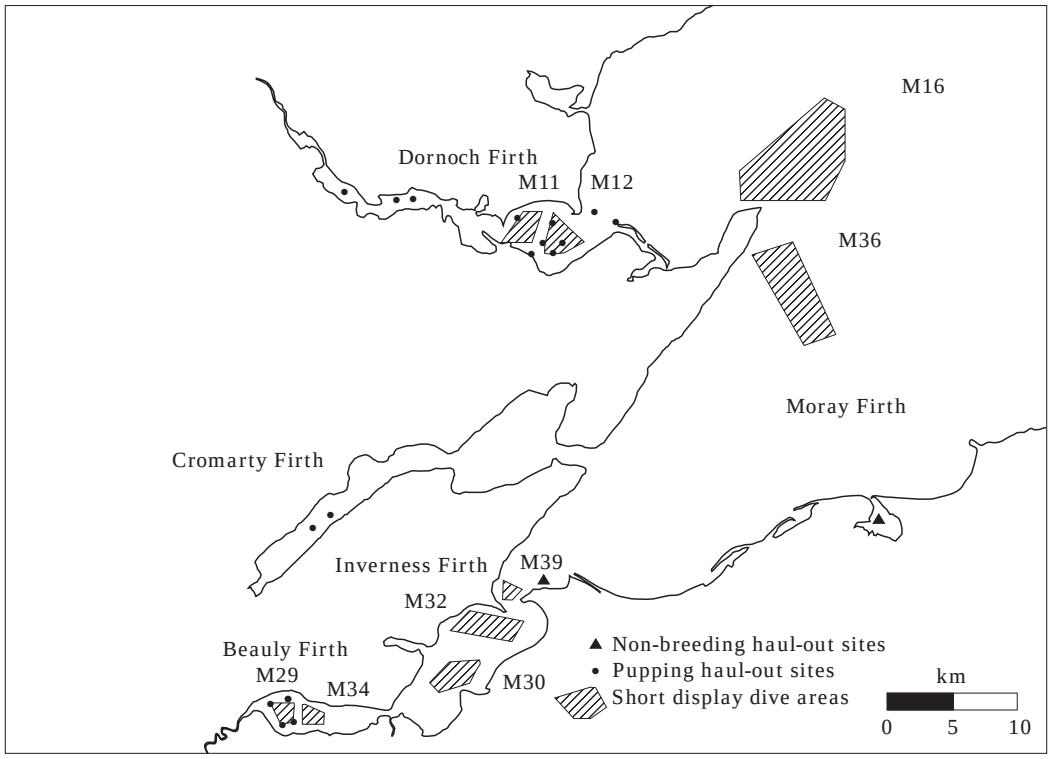

Figure 1. A map of the inner Moray Firth showing the locations of harbour seal haul-out sites and areas used by VHF-tagged males when making short display dives during the period in July when ranges were restricted.

We assessed spatial and temporal changes in the distribution of adult males using VHF radiotelemetry. Radiolocations were obtained by triangulation using hand-held directional aerials from coastal hilltops, and were accurate to $\pm 7.5^{\circ}$ (Thompson & Miller 1990). Between 1988 and 1994, seven of the 10 males were located once a day for at least 6 days a week. In 1995, three seals were located at least once during each feeding trip, and then more regularly during the mating period (see below). Estimates of range size were calculated for seals with daily locations ($N=7$) using the MCPAAL package (National Zoological Park, Smithsonian Institute, Washington, U.S.A.). We assessed changes in range size of these males before and during the breeding season 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 (Thompson et al. 1994). No account was taken of the possible error in locations in calculating range size. We used data from permanent recording stations (Nicholas et al. 1992) to estimate the amount of time which males spent hauled out each day (Thompson et al. 1989).

We determined dive durations and surfacing patterns of all 10 males from the pattern of VHF radio signals when these animals were located close to shore (Wanless et al. 1988; Nielsen 1995). We recorded these dive characteristics both manually while obtaining daily locations and using paper chart records from permanent receiving stations. Several males without radiotags were observed and recorded during related studies and showed similar dive and vocal behaviour to the radiotagged seals, suggesting that the application of a radiotag on the males did not greatly influence their behaviour. VHF signals could not be used to estimate dive durations when seals were feeding further offshore as the signals were often weak and broken. More detailed information on dive characteristics was available from the three seals fitted with recoverable time depth recorders (TDR) (Boyd & Croxall 1992). The resolution of

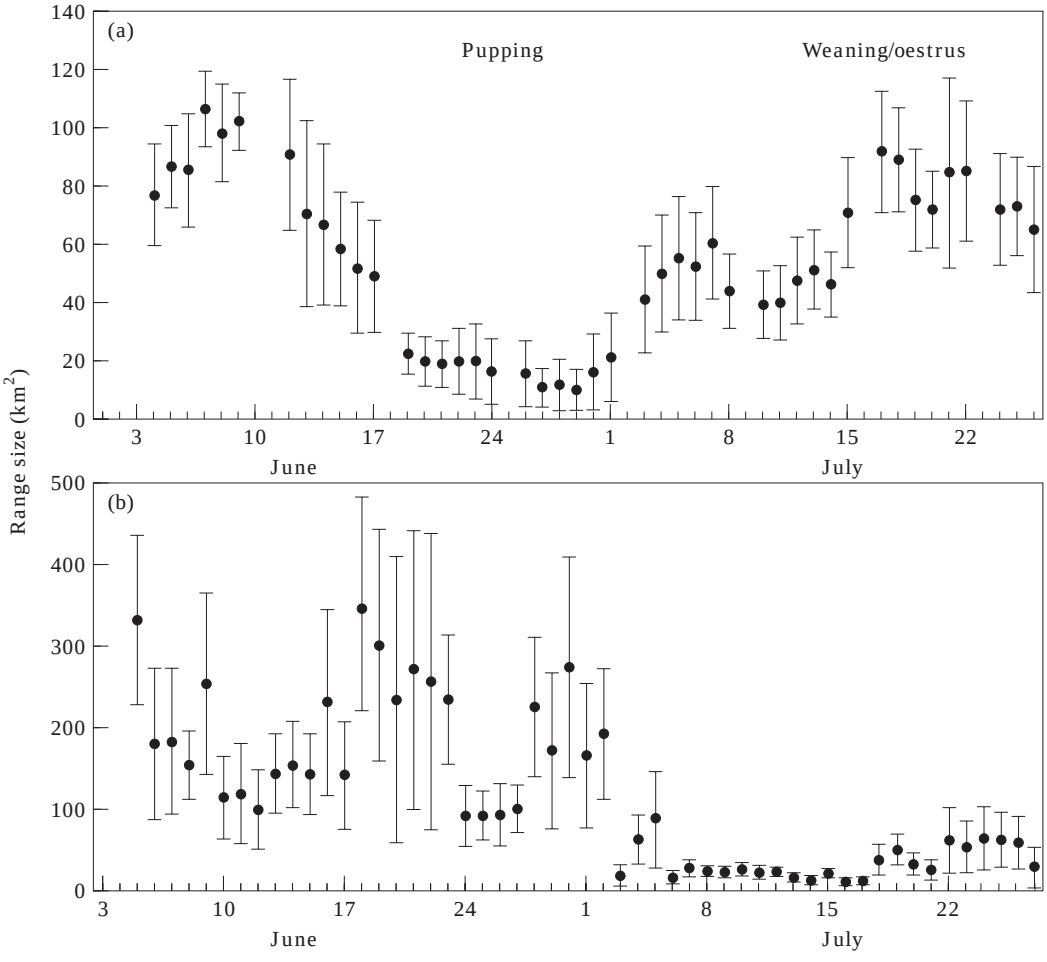

Figure 2. Variation in mean (± 1 SE) minimum convex polygon 7-day range sizes for (a) seven females with pups (re-drawn from Thompson et al. 1994); (b) seven male harbour seals. The mean for each day includes data from the 3 days either side. Consecutive points are therefore not independent.

the TDRs was 0.5 m and depth recordings were taken every 10 s. To rule out the possibility that we had missed short dives due to the 10-s sampling protocol, we inspected the depth profile of each dive and confirmed that the seals could not have reached the surface in between sample points. In doing so, we assumed a maximum swimming speed of 3 m/s which is approximately twice the minimum transport speed (Williams & Kooyman 1985).

Male Acoustic Behaviour

During the July mating period, we also located radiotagged seals from a 5.5 m boat on an opportunistic basis when weather conditions permitted. Once tagged individuals had been sighted, we recorded dive patterns (from the VHF signal) and acoustic behaviour. Acoustic recordings were obtained using a Sonobouy AN/SSQ-41A hydrophone and were recorded using a Digital Casio DT-90P recorder onto Sony DAT DA-7 tapes. We analysed calls using the SIGNAL sound analysis program (Engineering Design, Belmont, MA 02178, U.S.A.).

Female Distribution

A detailed analysis of the summer distribution of eight adult female seals has been made

elsewhere (Thompson et al. 1994). However, seven of these females were caught in only one of the pupping areas, the Dornoch Firth. To provide a more complete picture of female distribution, we include radiotracking data for a further six females caught in the Inverness Firth in 1992, 1993 and 1994.

RESULTS

Male Range Size

In June radiotagged males were widely dispersed, with mean 7-day ranges varying from 65 to 480 km^2. During the first week of July, males markedly decreased these ranges to around 4–70 km^2 (Fig. 2). In contrast to females (see Thompson et al. 1994) this decrease in range size did not result from an increase in the time that males spent hauled out during July. Median (inter-quartile range) daily haul-out durations (h) in June were 3.25 (0–8.0) compared with 1.0 (0–5.0) in July (Wilcoxon signed-ranks test statistic = 6.0, $N = 7$, NS).

Male Diving Behaviour

During July, when male ranges were smaller, males were often recorded making characteristically short dives. Typically, a long surface interval of 20–30 s was followed by a series of three to five short dives of around 60 s, each followed by brief surfacings of 1–4 s. This short series of dives was then followed by another longer surfacing and this pattern of diving was sometimes continued for several hours (Fig. 3). For the three seals fitted with TDRs, these dives were significantly shorter than the dives recorded during longer foraging trips earlier in the summer (Mann–Whitney U-test: M30, $U = 23\,783$, $N_{short} = 234$, $N_{long} = 2457$, $P < 0.001$; M34: $U = 110\,783$, $N_{short} = 614$, $N_{long} = 3279$, $P < 0.001$; M39: $U = 68\,842$, $N_{short} = 289$, $N_{long} = 1365$, $P < 0.001$; Fig. 4). Although data from foraging trips also showed the presence of short dives, these generally consisted of occasional short dives within a bout of longer dives. In contrast, the majority of dives recorded during July formed part of long repetitive bouts of short dives.

For three males (M30, M34, M39), it was possible to make direct observations and acoustic recordings while they were engaged in bouts of these short dives. M30 was recorded on one occasion for 60 min, while both M34 and M39 were recorded on 3 separate days, M34 for a total of 270 min and M39 for a total of 180 min. Each of the males made one or two vocalizations on the descent of each short dive. Preliminary acoustic analysis of these recordings showed that male vocalizations were typically low in frequency (mean frequency = 665 Hz, $N = 207$; Fig. 5). Most frequently ($N = 143$), calls consisted of a loud and pulsed burst of sound, the amplitude of which faded in and out at the start and end of the call.

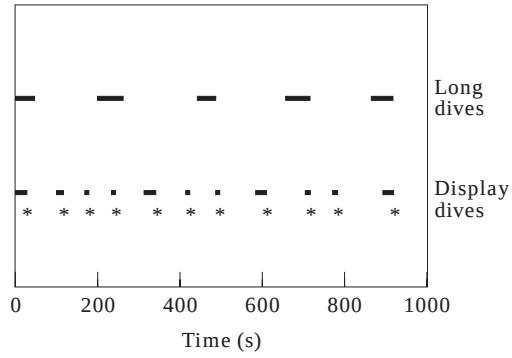

Figure 3. Differences in the surfacing patterns (■) of male M30 observed during bouts of long dives (6 June 1994) and display dives (19 July 1994). Vocalizations (*) occurred 5–6 s after the start of a display dive.

Distribution of Males and Females

Locations of the 14 radiotagged females during June and July show that female distribution was clumped around haul-out areas and those areas further out to sea which we assume are foraging areas (Fig. 6). Figure 1 shows the locations of male seals while they were making short dives during the period of their restricted range (5 July–11 August). Data on dive patterns during this period were not available for M1 in 1988, and he is therefore excluded from this analysis. The remaining nine males varied considerably in their choice of site. Compared with the female distribution (Fig. 6) some males were located in areas adjacent to haul-out sites in the Beauly Firth (M29, M34) and in the Dornoch Firth (M11, M12), while others were found much further out to sea near female foraging areas (M16, M36). Finally, several males were located in the Inverness Firth (M30, M32, M39) on transit

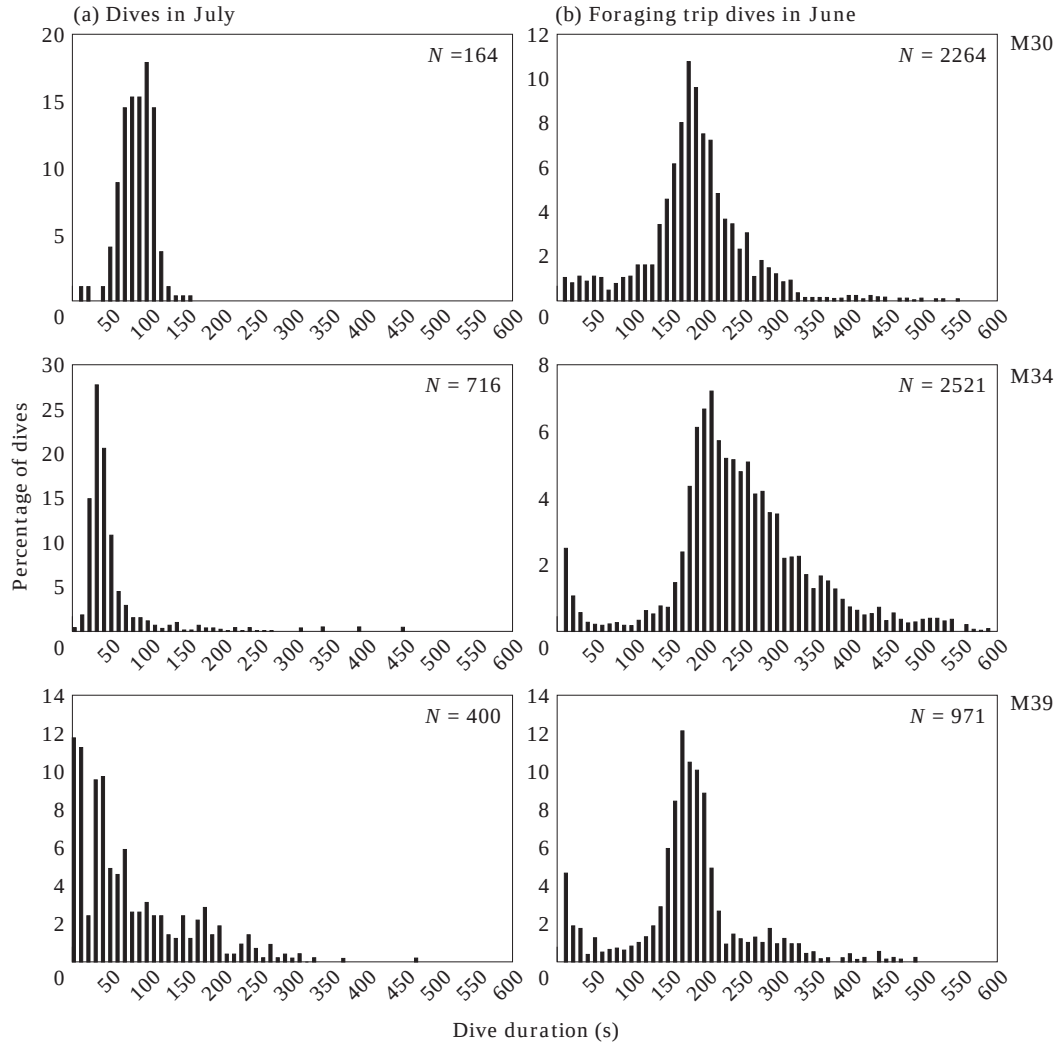

Figure 4. Frequency histograms of dive durations recorded from three males (a) during the July mating period and (b) during a foraging trip in June.

routes between female haul-out and foraging areas. Acoustic recordings were obtained from males in both the Beauly Firth haul-out area and the Inverness Firth. Logistic constraints prevented our confirming that seals located around foraging areas were also vocalizing.

DISCUSSION

Previous studies have shown that female harbour seals restrict their range during the early part of the lactation period (Fig. 2a), but that they make foraging trips in late lactation and are therefore widely dispersed when in oestrus (Boness et al. 1994, Thompson et al. 1994). Our study suggests that males continue to travel widely during the early pupping period, but then restrict their range at around the time that females start to make foraging trips in late lactation (Fig. 2b). Overall, males continued to spend similar amounts of time in the water during June and July. Distance from haul-out sites seemed to have no influence on male haul-out behaviour. M12 and M29 were located

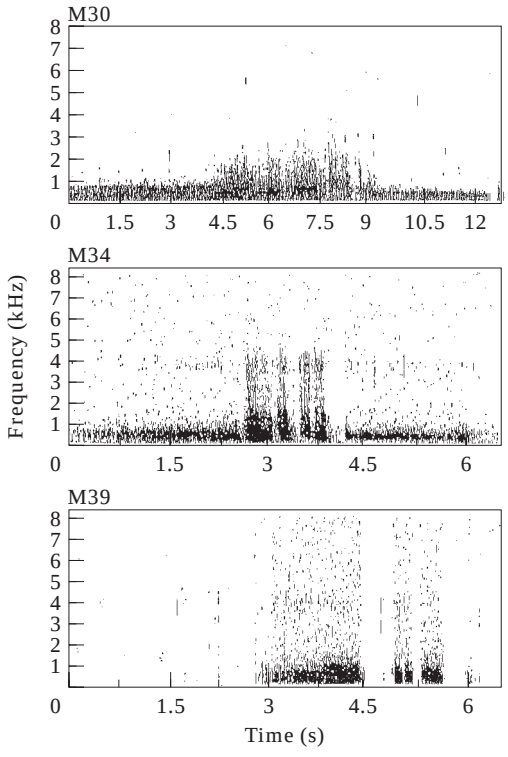

Figure 5. Sound spectrograms of vocalizations for three radiotagged males, M30, M34 and M39.

displaying next to haul-out sites but both hauled out less than some males that were located over transit routes or foraging areas.

Observations during the period when males restricted their range suggest that they were engaged in stereotypic diving and acoustic displays. Harbour seals have been observed making visual surface displays in several other studies (Sullivan 1981; Allen 1985; Perry 1993) and both these and stereotypic vocalizations (Hanggi & Schusterman 1994; Bjørge et al. 1995; D. Thompson, unpublished data) similar to those recorded in this study (Fig. 5) have been suggested to be associated with mating. Our data show that this display activity is associated with restrictions in range. Prior to this period we assume that males are foraging further offshore, and then switch to display behaviour when females are coming into oestrus and are ranging more widely.

Such displays could serve to defend preferred areas from other males and/or as an advertisement to females (Hanggi & Schusterman 1994). Our results show that males differ in the display areas that they use (Fig. 1). Different areas may have varying costs and benefits for male harbour seals during the mating season. Those around haul-out areas may provide easy access to a high and localized density of females. However,

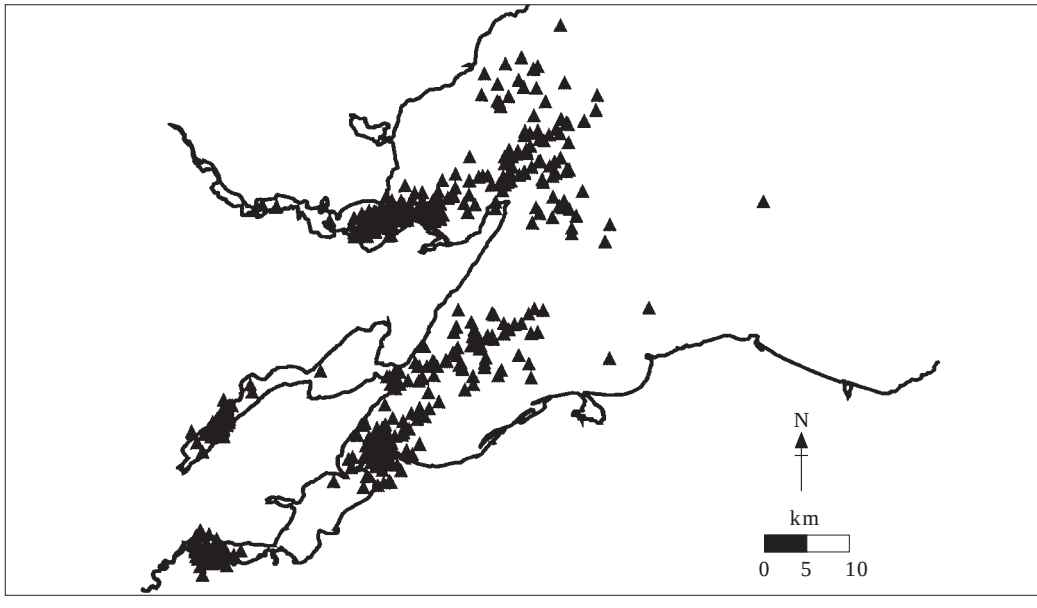

Figure 6. Daily locations of 14 adult female harbour seals during June and July of 1988–1994.

opportunities for foraging may be limited in these inshore areas (Thompson & Miller 1990) and males may have to fast during the period in which they are displaying. Studies in other areas have shown that adult male harbour seals lose condition during this period, and also suggest that foraging is restricted (Walker & Bowen 1993). In contrast, areas further offshore around female feeding grounds may provide a lower density of accessible females, and may offer greater options for males to feed in between bouts of displaying activity. Factors such as age, body size and condition could all influence which area a male uses during the mating season, and further work is needed to determine the causes and reproductive consequences of using these different display sites.

The mating system of the male harbour seal has been suggested to resemble that of a lek (Perry 1993; Hanggi & Schusterman 1994). Indeed, several indicators such as varying territory quality, visual and self-advertising displays and the occupation of small ranges by males for display, are all suggestive of lekking (Bradbury 1981; Balmford et al. 1992). Our study in particular tends to suggest that males may be using a system of dispersed but small display territories. However, the degree of clumping of displaying males within the areas used by females remains unclear, and we feel it is premature to suggest that harbour seals are lekking. It is now essential to obtain a better picture of the overall distribution and densities of displaying males. Previous studies have concentrated on observations of males around haul-out sites (Perry 1993; Hanggi & Schusterman 1994). Our study using VHF telemetry has shown that males may be displaying many kilometres from female pupping sites, and that future work on male reproductive strategies should be carried out over a much broader geographical area. Indeed, this conclusion is not restricted to those phocids that mate only at sea. Molecular techniques have similarly shown that an unexpectedly high proportion of grey seal pups were sired by males who were not the dominant individuals at the breeding sites (Amos et al. 1993). In the case of harbour seals, data linking display dives with acoustic displays suggest that a more complete picture of male distribution may now be obtained through wide scale acoustic surveys (Stirling et al. 1983; Cleator & Stirling 1990).

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