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SUMMER FORAGING ACTIVITY AND MOVEMENTS OF RADIO-TAGGED COMMON SEALS (*PHOCA VITULINA*. L.) IN THE MORAY FIRTH, SCOTLAND

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SUMMARY

(1) VHF telemetry was used to study summer foraging patterns and movements of three adult common seals (*Phoca vitulina* L.) in the Moray Firth, Scotland.

(2) Seals travelled up to 45 km from their haul-out sites on feeding trips of up to 6 days. Trip duration and foraging range were significantly correlated for all seals, although the precise form of this relationship differed between individuals.

(3) Harmonic mean analyses showed that at-sea locations were often clumped. Two individuals returned regularly to particular feeding areas, apparently associated with habitats such as rocky reefs and offshore sandbanks. Spatial and temporal variations in the distribution of seals are discussed in relation to their breeding activity and to changes in food availability.

INTRODUCTION

Information on the distribution of pinnipeds is based almost entirely on observations at terrestrial haul-out sites (Burns 1970; Bonner 1972). On the other hand, data on distribution are often required to interpret fishery interactions; for example, when assessing geographical variations in the extent of competition between seals and fisheries (Harwood 1987; Harwood & Croxall 1988). Clearly, if existing information on the terrestrial distribution of seals is to be used to evaluate such problems, data are required on the distance which seals travel from haul-out sites in order to feed.

Although direct observations of foraging seals can sometimes be made at sea, most have been made in inshore areas (Fisher 1952; Boyd 1962) or around commercial fishing activities (Rae 1968; Ryan & Maloney 1988). Similarly, previous studies using VHF radio-tracking techniques have tended to concentrate on activity and movements of seals in inshore haul-out areas (Pitcher & McAllister 1981; Brown & Mate 1983; Thompson 1989). In these studies, seals often travelled beyond the range of VHF radio-transmitters. Consequently, maximum foraging distances could not usually be determined and a representative sample of locations could not be obtained to identify preferred feeding areas. Even when longer range UHF satellite-transmitters have been deployed (McConnell 1986), the probability of locating a seal in the water has been low and few locations have been obtained of seals at sea.

In the present study, we used VHF telemetry to obtain data on the summer foraging patterns and movements of common seals (*Phoca vitulina* L.). Our primary aim was to obtain a representative sample of locations in order to produce estimates of foraging range and the duration of feeding trips for this species. In addition, we aimed to assess whether individual seals returned regularly to preferred feeding areas, and to identify any preferred feeding habitats.

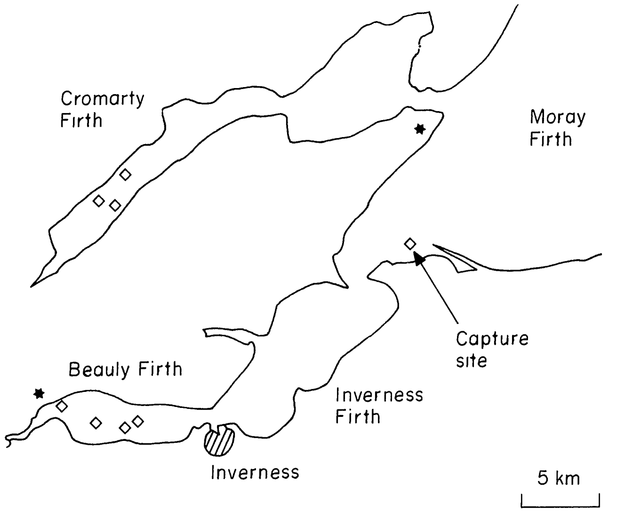

FIG. 1. Map of the study area showing the position of (◇) common seal haul-out sites and (★) permanent receiving stations.

METHODS

The study was carried out in the inner Moray Firth, north-east Scotland (Fig. 1), in the summer of 1988. In April, three adult common seals (two males and a pregnant female) were captured by running an inflatable boat onto an intertidal haul-out site. Once secured in a hoop-net, seals were sedated lightly using a mixture of ketamine-hydrochloride and vallium (Thompson 1989). A VHF radio-tag (173·2–173·35 MHz) was then glued to the hair on top of their heads using epoxy-resin (Fedak, Anderson & Curry 1983).

Radio-locations

From 15 May, until the radio-tags fell off at the beginning of the moult in July or August, seals were located daily. Locations were made at a randomized time of day or night to avoid biasing observations towards haul-out areas which may be used more frequently during the day (Boulva & McLaren 1979; Stewart 1984). Radio-fixes were made with a three-element Yagi aerial using the null-average method (Springer 1979). Only occasionally, when radio-signals were weak, could an acceptable fix be obtained using the loudest-signal method. The accuracy of fixes was estimated using a test transmitter at distances of 10–15 km, and the standard deviation of the error between estimated and true bearings used to produce 95% confidence limits for fixes on radio-tagged seals (Springer 1979). Locations were obtained by triangulation from vantage points on coastal roads and hill-tops. Where possible, we obtained at least three bearings (one during each of the three successive surface intervals) from each vantage point. The mean bearing from each vantage point was then used to estimate the seal's location and the size of the error polygon (Heezen & Tester 1967) was calculated using the 95% confidence limits around the mean.

The intensity with which seals used different parts of their home range was determined using the harmonic-mean model (Dixon & Chapman 1980) and calculated using the

MCPAAL package (National Zoological Park, Smithsonian Institute, Washington, U.S.A.).

Activity patterns

Data on the duration and timing of haul-out bouts and feeding trips were collected using two permanent receiving stations (Fig. 1). Each station contained a scanning receiver which could receive signals from radio-tagged seals at a range of up to 20 km. The frequency of each seal's transmitter was monitored for at least one 16-minute sampling period h^{-1} and signals were recorded on a paper chart recorder. Because VHF signals were heard only when the seal was at the surface or on land, each seal's activity could be classified as either diving or hauled-out. When seals moved out of range of the stations we assumed that they were diving. Daily locations using hand-held Yagi aerials confirmed that seals did not haul-out at sites outside the range of the receiving stations.

Chart records were used to produce daily activity summaries for each individual (Thompson *et al.* 1989). The duration of feeding trips (i.e. all periods spent in the water) and haul-out bouts were then measured from these summaries.

The relationship between feeding trip duration and foraging range was investigated using data from trips where a radio-fix was obtained in the middle 80% of the trip. Fixes made early or late in the trip were ignored in order to avoid using locations of travelling seals and thus underestimating foraging range. Foraging range was estimated using minimum straight-line distances between haul-out sites and feeding locations, and confidence limits were obtained from the size of the error polygon (Springer 1979).

The effect of circadian and tidal cycles on the timing of haul-out bouts was assessed using circular statistics. The mid-point of each haul-out bout was converted to two angles; one corresponding to the time of day (where one 24-h cycle = 360°), the other to the state of the tide (one high tide to the next high tide = 0–360°). Watson's *U*-test (Batschelet 1981) was used to test whether the timing of haul-out bouts was random with respect to the time of day or to the tidal cycle. When a significant deviation from randomness was shown, the mean hour and stage of the tide were also calculated (Batschelet 1981).

RESULTS

Locations were obtained for each seal on all except 3 days, when we were unable to obtain a precise fix on one individual. Nevertheless, even on these days we were able to establish that the seal was within the broad area that it used throughout the rest of the study. We are therefore confident that these locations were representative of the three seals' home ranges over the period that they were tracked (Fig. 2) and that we did not miss longer distance movements.

Daily locations and 95%, 75% and 50% harmonic mean isoclines are shown for each individual in Fig. 2. Trials with a test-transmitter showed that 95% confidence intervals for single radio-fixes were $\pm 12°$ of the estimated bearing and $\pm 7{\cdot}5°$ where the mean of three estimates of the seal's position was used. Ninety per cent of the resulting 95% error polygons were < 25 km^2 in area, and all were less than 100 km^2.

For all three seals there was a cluster of locations around the haul-out site at which they had been caught and, in the case of the female, around a second group of haul-out sites that she used in the Beauly Firth. Locations made while seals were diving were sometimes also within these haul-out areas, but most were further east towards more open sea. Maximum recorded distances travelled between haul-out sites and feeding areas were

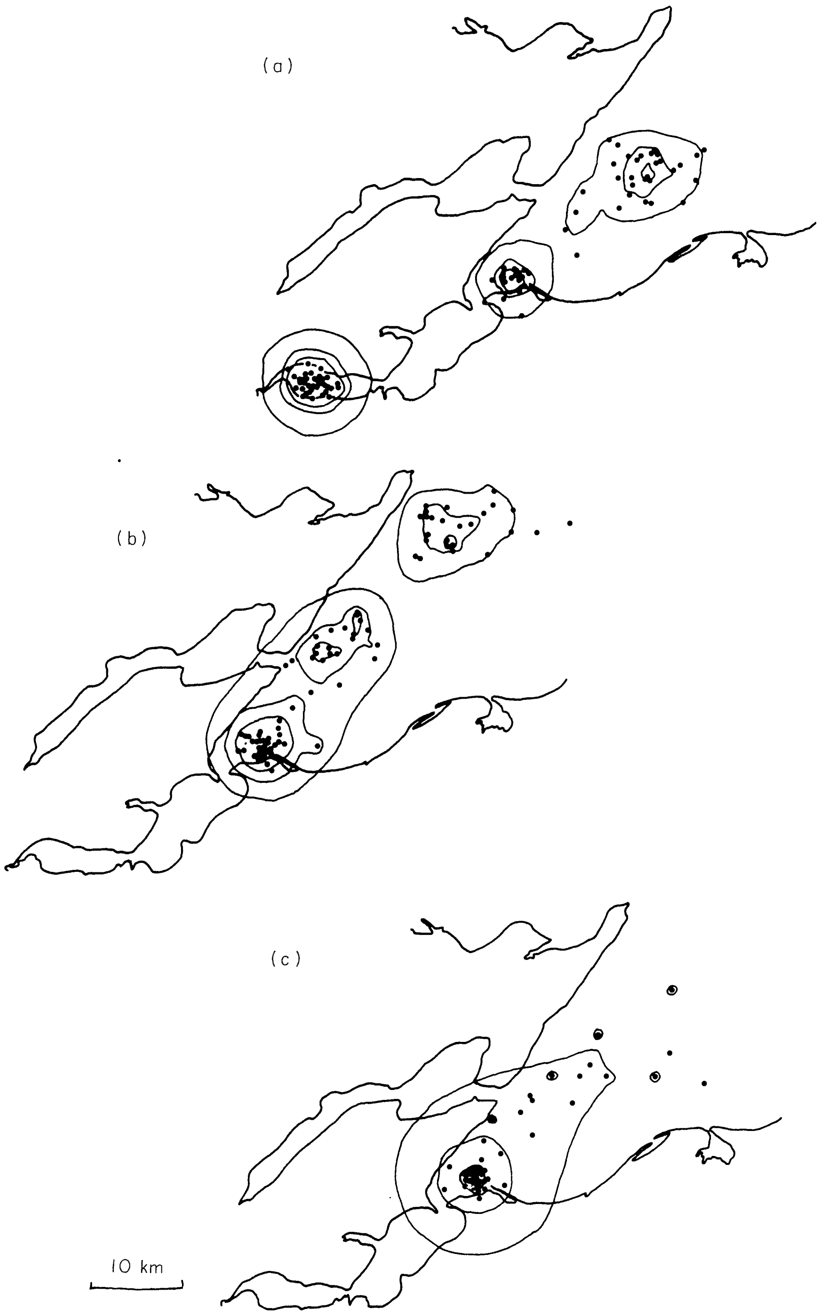

FIG. 2. Daily locations of radio-tagged seals with 95%, 75% and 50% harmonic mean isoclines: (a) female, 14 May–7 Aug 1988; (b) male 1, 14 May–30 July 1988; (c) male 2, 14 May–7 July 1988.

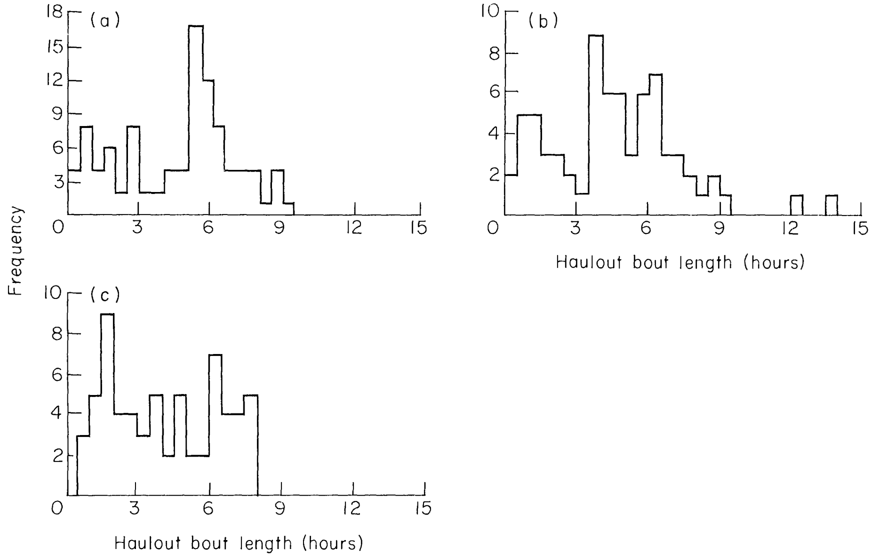

FIG. 3. Frequency distributions for haul-out bout lengths: (a) female, (b) male 1, (c) male 2.

TABLE 1. Results of Watson's *U*-test and descriptive circular analyses used to assess the effect of time of day and the tidal cycle on the behaviour of radio-tagged seals: (a) time of day, (b) tidal cycle. Mean tide state is expressed in degrees, i.e. high tide = 0 and 360, low tide = approx 180

	U	*n*	Mean time	*r*	*P*
(a) Female	0·12	99	—	—	N.S.
Male 1	0·51	71	13·58	0·37	<0·01
Male 2	0·32	64	14·21	0·30	<0·01
			Mean tide state		
(b) Female	2·24	99	184	0·61	<0·01
Male 1	1·89	71	171	0·71	<0·01
Male 2	1·06	64	170	0·56	<0·01

46 km, 38 km and 25 km for the female, male 1 and male 2, respectively. Male 2 showed a dispersed distribution while at sea. On the other hand, both the female and male 1 showed a clustered distribution of locations at sea. The centre of the female's cluster lay near an offshore sandbank, while male 1's locations fell into two groups. The first area, just off the mouth of the Cromarty Firth, was used by male 1 until 20 June. After this, he was located regularly in the north-east part of the study area, close to a rocky reef.

On three occasions, male 1 was located at sea shortly before he returned to haul-out. The time at which he arrived at the haul-out site was recorded by the receiving station, giving estimates of 4·95–5·19, 5·19–5·89 and 4·41–5·09 km h^{-1} for his minimum swimming speed on his return journey. Repeated locations of seals in the same feeding

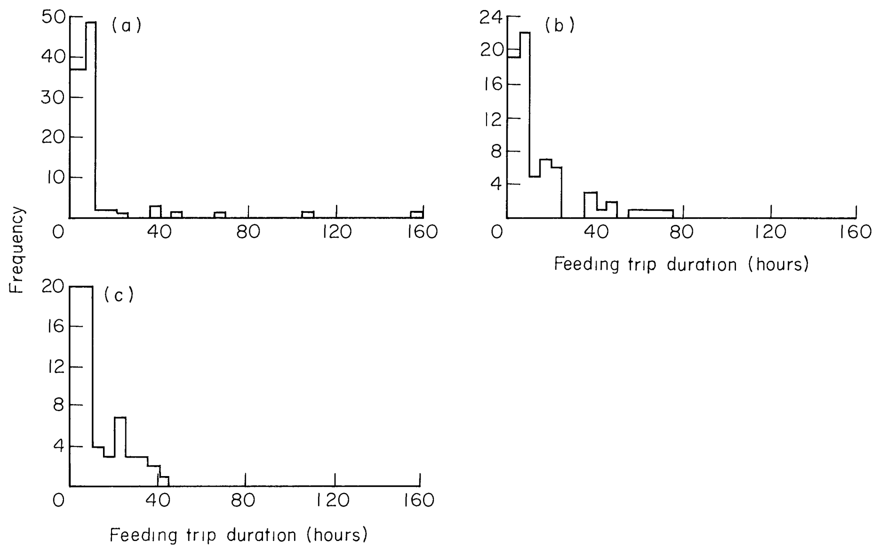

FIG. 4. Frequency distributions for foraging trip durations: (a) female, (b) male 1, (c) male 2.

TABLE 2. Data on the proportion of time that radio-tagged seals were hauled out, and the proportion of their time in the water on short (< 12 h) and long (> 12 h) feeding trips. n = the number of days with complete activity records

	Proportion of time hauled out	Proportion of time on short trips	Proportion of time on long trips	n
Female	0·25	0·34	0·41	75
Male 1	0·18	0·18	0·64	72
Male 2	0·24	0·23	0·53	50

area on subsequent days, and the rapid return journeys recorded for male 1, suggest that individuals swam directly to and from their feeding areas.

Haul-out bouts were only occasionally longer than 8 h (Fig. 3), and the timing of bouts was significantly correlated with the tidal cycle for all three seals (Table 1). Both males also showed a significant diurnal haul-out pattern, with maximum haul-out activity occurring in the middle of the afternoon (Table 1).

The duration of most feeding trips was less than 12 h (Fig. 4). However, all three individuals made much longer trips, of up to 6 days, and these long trips accounted for a high proportion of the total amount of time that seals spent in the water (Table 2). Long feeding trips also tended to involve longer distance movements, and there was a significant relationship between trip duration and the minimum distance travelled for all three seals (Fig. 5).

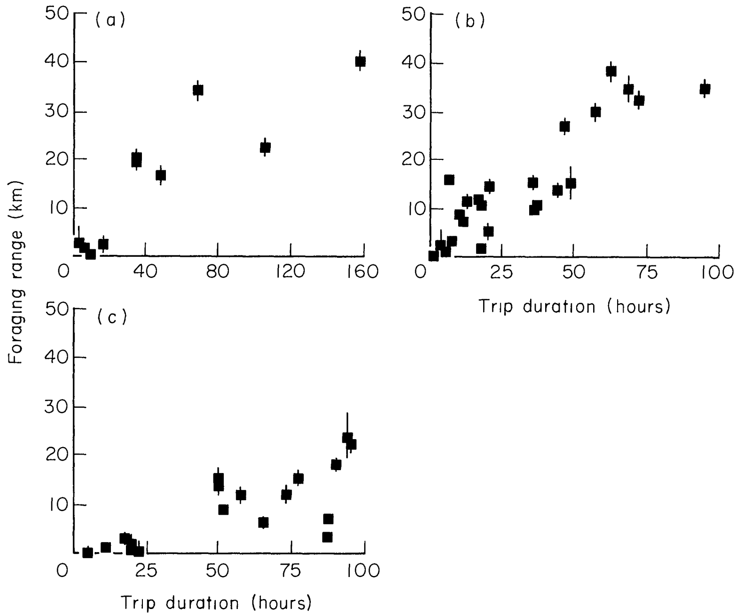

FIG. 5. Relationship between minimum foraging range (km) and trip duration (h). (a) Female: $y=2{\cdot}4+0{\cdot}27\ x$, $r=0{\cdot}89$, $P<0{\cdot}001$. (b) Male 1: $y=2{\cdot}0+0{\cdot}41\ x$, $r=0{\cdot}89$, $P<0{\cdot}001$; (c) Male 2: $y=0{\cdot}50\ x-1{\cdot}0$, $r=0{\cdot}77$, $P<0{\cdot}001$.

DISCUSSION

These results show that VHF telemetry can be used to follow the movements at sea of pinnipeds inhabiting inshore waters, although the success of this technique is likely to depend on the nature of the study area. In the Moray Firth, our study area was relatively enclosed, fringed with coastal hills and a good network of public roads. In contrast, during similar studies in Orkney (Thompson 1989) it was often impossible to determine the location of foraging seals due to the lack of suitable coastal vantage points. In addition, one apparent disadvantage of obtaining radio-locations from land was that errors around individual locations were sometimes large. However, we feel that, once quantified, such errors are relatively unimportant given the long distances that seals were travelling to feed and the clumped distribution of most feeding locations.

Our estimates of foraging range are in line with previous suggestions that common seals are coastal feeders, rarely occurring further than a few kilometres offshore (Spalding 1964; Rae 1968). Nevertheless, although they appear to remain in coastal waters, these data show that this species regularly moves distances of up to 45 km from their haul-out sites on feeding trips of up to 6 days' duration. Longer distance movements of individually marked seals have been identified in other studies. However, such movements appear to be dispersal movements by young seals (Bonner & Witthames 1974; Thompson 1989), or seasonal movements between different haul-out areas (Allen 1988) and are therefore not directly comparable with our estimates of foraging range.

Comparative data on feeding locations of other pinnipeds are rare. In a study of northern fur seals (*Callorhinus ursinus* L.), three radio-tagged females were each followed for one complete feeding trip using a research vessel and a larger sample was located during aerial surveys (Loughlin, Bengtson & Merrick 1987). The duration of fur seal feeding trips was similar (3·5–9·7 d) to those observed in common seals during this study, although fur seals travelled much further (160–200 km) to feed. Loughlin, Bengtson & Merrick (1987) also suggested that female fur seals returned to the same area on successive feeding trips; only one female was located in a feeding area on two occasions, but all the individuals followed swam to feeding areas on a direct route. Data collected in the present study showed that two individuals returned regularly to particular areas (Fig. 2), with one seal (male 1) showing a change in his preferred area during the study. We suspect that such preferences were associated with areas of rocky reef (male 1) and sandbank (female), known to be important for local fisheries and sea-angling.

Interpretation of data on the aquatic distribution of seals is restricted because we cannot assume that seals foraged all the time they were in the water. Haul-out activity in the Moray Firth was limited to bouts of a few hours over single low-tide periods (Fig. 3). In contrast, haul-out bouts of > 24 h have been recorded in other areas where haul-out sites are available throughout the tidal cycle (Yochem *et al.* 1987; Allen 1988). Many of the short feeding trips could therefore have been resting bouts spent in the water between two low-tide haul-out bouts. Although these short periods in the water were most frequent (Fig. 4) they accounted for only a relatively small proportion of the total time that radio-tagged seals spent in the water (Table 2). Longer trips may therefore represent the more important foraging activity, when seals also travelled further from haul-out sites (Fig. 5). The use of time–depth recorders (TDRs) to collect data on the diving patterns of several otariid species has shown that long feeding trips often consist of a number of foraging bouts interspersed with periods of rest (Croxall *et al.* 1985; Gentry & Kooyman 1986). The longer feeding trips seen in this study could also have consisted of several bouts of foraging activity, with intervening periods of rest in the feeding areas. The tendency for the two males to spend more time hauled-out during the day (Table 1) may indicate that foraging bouts were more likely to occur at night. Similar haul-out patterns have been observed in other studies of pinnipeds and it has been suggested that seals feed nocturnally in response to nocturnal changes in the vertical distribution or schooling behaviour of their prey (Trillmich & Mohren 1981; Croxall *et al.* 1985; Thompson *et al.* 1989). The much stronger (as indicated by the relative r values in Table 1) influence of the tidal cycle on haul-out behaviour is likely to result primarily from changes in site availability, although the tidal cycle could also be influencing food availability through tide-related changes in fish activity (Gibson 1978).

In summer, the aquatic distribution of common seals could also be related to breeding activity. Determining the relative effect of breeding and feeding activities on common seal distribution was particularly difficult for males, as we had no independent measure of breeding status for the males that we captured. Mating takes place in the water and little sexual activity is seen at haul-out sites (Allen 1985; Thompson 1988). Consequently, we would predict that, during and leading up to the July mating period, breeding males should spend their time in areas of water where they are likely to encounter adult females. The radio-tagged female, and most other females with pups, used haul-out sites in the inner parts of the Beauly and Cromarty Firths during the lactation period (Fig. 1). Male 1 and male 2 continued to use a site outside these areas throughout the study and we suspect both may have been non-breeders, with most at-sea locations representing foraging trips. However, male 1's repeated locations in the mouth of the Cromarty Firth in the early part of the season could be interpreted as potential breeding activity, particularly if females moved regularly between haul-out sites in the Cromarty Firth and feeding areas in the outer firth.

As predicted by central place foraging theory (Orians & Pearson 1979), seals tended to remain longer in more distant feeding areas (Fig. 5). Similarly, a significant positive relationship was found between trip duration and transit times using data from TDRs deployed on four species of otariid (Gentry & Kooyman 1986). In most situations where data are required on pinniped foraging ranges it is likely to be simpler to estimate the duration of feeding trips than it would be to follow individual seals to feeding areas. At first sight, it appears that one could use data on trip durations to estimate foraging range. However, data from the present study show that, although the relationship between trip duration and foraging range was significant for each individual, the slope of the relationship differed between individuals (Fig. 5). Similarly, the fit for the otariid data was best when species means were used and rather poor when analysed for individuals (Gentry & Kooyman 1986). Although such variation suggests that the use of this relationship to estimate foraging range would be unwise, the causes behind it are of interest. In particular, the slope of the relationship may be influenced by changes in the cost of travel, for example due to differences in body size or shape (Williams & Kooyman 1985; Feldkamp 1987), or by food availability or foraging success in different feeding areas. Further study of this relationship over a range of individuals may provide a useful insight into common seal foraging energetics.

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REFERENCES

Allen, S. G. (1985). Mating behaviour in the harbor seal. *Marine Mammal Science*, **1**, 84–87.

Allen, S. G. (1988). *Movement and activity patterns of harbor seals at Point Reyes Peninsula, California*. M. Sc. thesis, University of California, Berkeley.

Batschelet, E. (1981). *Circular Statistics in Biology*. Academic Press, London.

Bonner, W. N. (1972). The grey seal and common seal in European waters. *Oceanography and Marine Biology Annual Review*, **10,** 461–507.

Bonner, W. N. & Witthames, S. R. (1974). Dispersal of common seal (*Phoca vitulina*), tagged in the Wash, East Anglia. *Journal of Zoology*, **174,** 528–531.

Boulva, J. & McLaren, I. A. (1979). Biology of the harbor seal, *Phoca vitulina*, in eastern Canada. *Bulletin of the Fisheries Research Board of Canada*, **200,** 24pp.

Boyd, J. M. (1962). Seasonal occurrence and movements of seals in north-west Britain. *Proceedings of the Zoological Society of London*, **138,** 385–404.

Brown, R. F. & Mate, B. R. (1983). Abundance, movements and feeding habits of harbor seals, *Phoca vitulina*, at Netarts and Tillamook Bays, Oregon. *Fishery Bulletin*, **81,** 291–301.

Burns, J. J. (1970). Remarks on the distribution and natural history of pagophilic pinnipeds in the Bering and Chukchi Seas. *Journal of Mammalogy*, **51,** 445–454.

Croxall, J. P., Everson, I., Kooyman, G. L., Ricketts, C. & Davis, R. W. (1985). Fur seal diving behaviour in relation to vertical distribution of krill. *Journal of Animal Ecology*, **54,** 1–8.

Dixon, K. R. & Chapman, J. A. (1980). Harmonic mean measure of animal activity areas. *Ecology*, **61,** 1040–1044.

Fedak, M. A., Anderson, S. S. & Curry, M. G. (1983). Attachment of a radio tag to the fur of seals. *Journal of Zoology*, **200,** 298–300.

Feldkamp, S. D. (1987). Swimming in the California Sea Lion: morphometrics, drag and energetics. *Journal of Experimental Biology*, **131,** 117–135.

Fisher, H. D. (1952). The status of the harbour seal in British Columbia, with particular reference to the Skeena River. *Bulletin of the Fisheries Research Board of Canada*, **93,** 58 pp.

Gentry, R L. & Kooyman, G. L. (1986). *Fur Seals: Maternal Strategies on Land and at Sea*. Princeton University Press, New Jersey.

Gibson, R. N. (1978). Lunar and tidal rhythms in fish. *Rhythmic Activity of Fishes* (Ed. by J. Thorpe), pp. 201–214. Academic Press, London.

Harwood, J. (1987). Competition between seals and fisheries. *Science Progress*, **71,** 429–437.

Harwood, J. & Croxall, J. P. (1988). The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic. *Marine Mammal Science*, **4,** 13–33.

Heezen, K. L. & Tester, J. R. (1967). Evaluation of radio-tracking by triangulation with special reference to deer movements. *Journal of Wildlife Management*, **31,** 124–141.

Loughlin, T. R., Bengtson, J. L. & Merrick, R. L. (1987). Characteristics of feeding trips of female northern fur seals. *Canadian Journal of Zoology*, **65,** 2079–2084.

McConnell, B. J. (1986). Tracking grey seals, *Halichoerus grypus*, using Service Argos. *Mesogee*, **46,** 93–94.

Orians, G. H. & Pearson, N. E. (1979). On the theory of central place foraging. *Analysis of Ecological Systems* (Ed. by D. J. Horn, R. D. Mitchell & R. G. Stairs), pp. 155–177. Ohio State University Press, Columbus.

Pitcher, K. W. & McAllister, D. C. (1981). Movements and behaviour of radio-tagged harbour seals, *Phoca vitulina*. *Canadian Field Naturalist*, **95,** 292–297.

Rae, B. B. (1968). The food of seals in Scottish waters. *Marine Research*, **2,** 1–23.

Ryan, P. C. & Maloney, C. L. (1988). Effect of trawling on bird and seal distributions in the southern Benguela region. *Marine Ecology Progress Series*, **45,** 1–11.

Spalding, D. J. (1964). Comparative feeding habits of the Fur Seal, Sea Lion and Harbour Seal on the British Columbia Coast. *Bulletin of the Fisheries Research Board of Canada*, **146,** p. 55.

Springer, J. T. (1979). Some sources of bias and sampling error in radio-triangulation. *Journal of Wildlife Management*, **43,** 926–935.

Stewart, B. S. (1984). Diurnal hauling patterns of harbor seals at San Miguel Island, California. *Journal of Wildlife Management*, **48,** 1459–1461.

Thompson, P. M. (1988). The timing of mating in the common seal, *Phoca vitulina*. *Mammal Review*, **18,** 105–112.

Thompson, P. M. (1989). Seasonal changes in the distribution and composition of common seal *Phoca vitulina* haul-out groups. *Journal of Zoology*, **212,** 597–603.

Thompson, P. M., Fedak, M. A., McConnell, B. J. & Nicholas, K. S. (1989). Seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*). *Journal of Applied Ecology*, **26,** 521–535.

Trillmich, F. & Mohren, W. (1981). Effects of the lunar cycle on the Galapagos fur seal, *Arctocephalus galapagoensis*. *Oecologia*, **48,** 85–92.

Williams, T. M. & Kooyman, G. L. (1985). Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. *Physiological Zoology*, **58,** 576–589.

Yochem, P. K., Stewart, B. S., DeLong, R. L. & DeMaster, D. P. (1987). Diel haul-out patterns and site fidelity of harbor seals (*Phoca vitulina richardsi*) on San Miguel Island, California, in autumn. *Marine Mammal Science*, **3,** 323–333.

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