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FINE SCALE TOPOGRAPHIC INFLUENCES ON ENVIRONMENTAL POTENTIAL FOR POLYGAMY (EPP) IN GREY SEALS

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INTRODUCTION. Emlen and Oring (1977) proposed that certain environmental factors determine the degree to which mates can be monopolised and thus define the environmental potential for polygamy (EPP). The primary environmental factor identified was the spatio-temporal dispersion of resources or receptive females. Where females are uniformly distributed in space, there is little opportunity for monopolisation of mates (low EPP); where females are aggregated, EPP is greater. The degree of synchrony of oestrus forms the temporal component to EPP. Moderate synchrony enhances EPP, whilst both extreme synchrony (individual males are unable to mate with females simultaneously) and extreme asynchrony (males are less likely to maintain positions amongst breeding females for extensive periods) depress EPP.

Female grey seals (*Halichoerus grypus*) gather annually at remote, usually offshore islands to give birth to a single pup and, after weaning the pup, to mate. Within colonies, grey seals exhibit moderate synchrony of oestrus, having discrete breeding seasons of approximately two months duration, with each female present for approximately 19 days, the period from parturition to weaning. Male grey seals have sufficient energy reserves to maintain positions on the colony for the entire breeding season and compete aggressively for access to oestrus females. Thus, the size, density and temporal coherence of female groups on breeding colonies will be the primary determinant of EPP in this species.

As the spatio-temporal dispersion of resources and/or females may differ between populations, Emlen & Oring (1977) anticipated “considerable lability” in mating systems, with intra-specific variation in EPP and consequently the intensity of sexual selection and the degree of polygyny. Grey seals breed on a wide variety of substrates (Stirling 1975), which may differentially constrain or promote spatial aggregation. Here we test fine scale topographic influences on breeding female spatio-temporal dispersion at two topographically differing Scottish colonies; North Rona (59°06'N, 05°50'W) and the Isle of May (56°11'N, 02°33'W). We use high resolution images from aerial photography within a GIS to provide accurate quantification of breeding female dispersion patterns and thus estimate the relative EPP at these sites and make predictions concerning the expected differences in degree of polygyny.

MATERIALS AND METHODS. Large format colour aerial photographs of our two study colonies (Hiby *et al.* 1988), taken on four dates during the 1994 breeding season at the Isle of May and five dates at North Rona, were scanned as high resolution images. Images were registered and rectified to real world co-ordinates within a GIS (ARC-INFO Version 7.0.3: ESRI, 380 New York Street, Redlands, Ca., USA) using sub-meter accurate ground control points derived in the field with Carrier Phase Differential GPS. Rectified images had pixel sizes equivalent to approximately 5cm x 5cm on the ground. Locations and sex-age class of all seals were digitised from these images. Overlapping images, used as stereo-pairs, provided sub-meter accurate Digital Elevation Models (DEMs) of the sites with measures of elevation and slope in 2m grid cells (Mills *et al.* 1997). Observations suggest that access to water may be an important determinant of pupping site selection. Therefore, we used GIS cost-surface functions to generate indices for each grid cell within the DEMs indicating the relative cost of moving from that

location to the nearest pool or access point to the sea (as digitised from the images). Indices were based on least-cost routes incorporating modifiers for the surface features traversed or topographical barriers circumnavigated. GRID based functions of the GIS were used to compare topographical parameters between colonies and, within colonies, between areas containing breeding seals and areas where seals were absent.

Breeding female dispersion patterns through the breeding season were compared between colonies using the spatial tools of the GIS. Frequency distributions of the numbers of females in 10m quadrats were compared against random and negative binomial distributions to examine the degree of spatial aggregation. In addition, for each coverage of breeding females, individuals were classified according to their nearest male. These arbitrary groupings were designed to assess female group size based solely on proximity to males. Frequency distributions of group sizes for each colony and date were compared.

Pupping curves from both study colonies (derived from direct observations of pup numbers during 1994) were used to calculate the number of new pups born on each date through the breeding season. These were converted to estimates of the number of females in oestrus per day by displacing the resulting curve by 19 days to the right on the abscissa. This provided an estimate of changes in the temporal availability of receptive females.

RESULTS. We examined the standard deviation in slope values observed in neighbouring grid cells for each cell in our DEMs. This process was repeated at grid cell resolutions ranging from 10 to 50m and revealed that local variation in slope at North Rona remained relatively constant irrespective of the spatial scale at which it was measured. This indicates that the terrain at North Rona is relatively even. By contrast the Isle of May is more broken and rugged, showing significantly greater variation in slope (Mann-Whitney U tests, significant at $p < 0.001$) at all grid cell resolutions.

Female location was dictated by topography (see also Pomeroy *et al.* 1994). Compared to unoccupied areas, sites containing breeding seals were at significantly lower elevations, on shallower slopes and had relatively easy access to either the sea (Mann-Whitney U: Isle of May; $z = -3.9$, $n = 26039$, $p < 0.001$, North Rona; $z = -5.6$, $n = 27450$, $p < 0.0001$) or pools of water (Isle of May; $z = -10.7$, $n = 27536$, $p < 0.001$, North Rona; $z = -20.9$, $n = 27450$, $p < 0.0001$).

Female dispersion patterns at both sites were random at the onset of the season, but became aggregated around the peak pupping date (variance \gg mean, significant differences from Poisson distribution, $1/k$ values ranging from 4.2 to 9.0 at the Isle of May and 3.9 to 6.2 at North Rona) with maximum aggregation occurring mid-season, between peak pupping and peak oestrous dates (Fig. 1). Female aggregation was significantly greater at the most topographically rugged site (Isle of May) than at the less rugged colony (North Rona). This difference was maintained throughout the breeding season (Fig. 1) (ANOVA with Scheffe's Multiple range test for nearest neighbour distances for females: $F_{8,2355} = 35.69$, $p < 0.0001$).

Operational sex-ratios, as observed from the coverages were more skewed at the Isle of May than at North Rona (Table 1). Female groupings based on proximity to individual males at these sites also showed significant differences between colonies with larger groups at the Isle of May than at North Rona until the end of the breeding season (Table 1) (ANOVA with Scheffe's Multiple range test for female group size: $F_{8,250} = 12.43$, $p < 0.0001$).

There were notable differences between the two colonies in the temporal availability of receptive females (Fig. 2). The Isle of May had a single sharp peak of high availability of oestrus

females. By contrast the period of high availability of oestrus females at North Rona is more extended with a secondary peak of availability in the latter half of the season.

DISCUSSION. Broad scale topographic influences on pinniped dispersion patterns within and between breeding colonies have long been acknowledged (Bartholomew 1970, Stirling 1975, Boness 1991, Le Boeuf 1991), however few studies have provided accurate quantitative measures of dispersion patterns (e.g. Baldi *et al.* 1996) and most rely on qualitative comparisons of topography. Our use of high resolution aerial photography within a GIS has allowed the accurate mapping of dispersion patterns and topography.

Breeding females at the Isle of May were spatially more aggregated than those at North Rona throughout the breeding season. This was largely as a consequence of the differing topographies. The more rugged, broken terrain at the Isle of May lead to tighter groups of females, whilst the relatively open grassy lawns of North Rona allowed females to be more dispersed. Viewed simply from the perspective of spatial aggregation, these result indicate a greater EPP at the Isle of May than at North Rona. This interpretation is supported by the observed differences in sex ratios and female groupings based on proximity to males. Greater clustering of females promotes male exclusion by resident males and leads to more skewed sex ratios (Bartholomew 1970). If EPP predicts the actual degree of polygyny these results suggest more extreme polygyny at topographically rugged sites than at less rugged sites. However, preliminary results from extensive molecular studies (unpubl. data. W. Amos & J. Worthington-Wilmer, Cambridge Univ.) show no significant differences in the degree of polygyny between these two colonies. Therefore, male reproductive success may not reflect variation in group size as determined by topography. This suggests that either (i) EPP is not being capitalised upon by males, perhaps due to factors such as inter-annual mate fidelity (Amos *et al.* 1995), or (ii) the relationship between the relative timing of maximal spatial aggregation and of temporal availability acts to moderate EPP at both sites (i.e. comparing spatial aggregations without regard to the temporal aspect may give misleading indications of the relative EPP). At the Isle of May, where females are more spatially aggregated (therefore relatively high EPP in spatial terms), the temporal spread of high availability of females is relatively short, giving individual males relatively less time during which to capitalise upon the high 'spatial' EPP (thus, reducing EPP overall). Conversely, at North Rona, females are spatially more dispersed (lower 'spatial' EPP) but with a longer temporal spread of high availability of oestrus females (higher 'temporal' EPP). Thus, although the spatio-temporal dispersion patterns do differ between these colonies, such intra-specific plasticity in behaviour may result in similar levels of EPP and, consequently, degrees of polygyny.

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Table 1. Seasonal changes in mean natural log transformed female group size + 1 (based on proximity to males - see text) at the Isle of May and North Rona in 1994. Sex ratios are expressed as males:females. Date is expressed as number of days relative to peak pupping date.

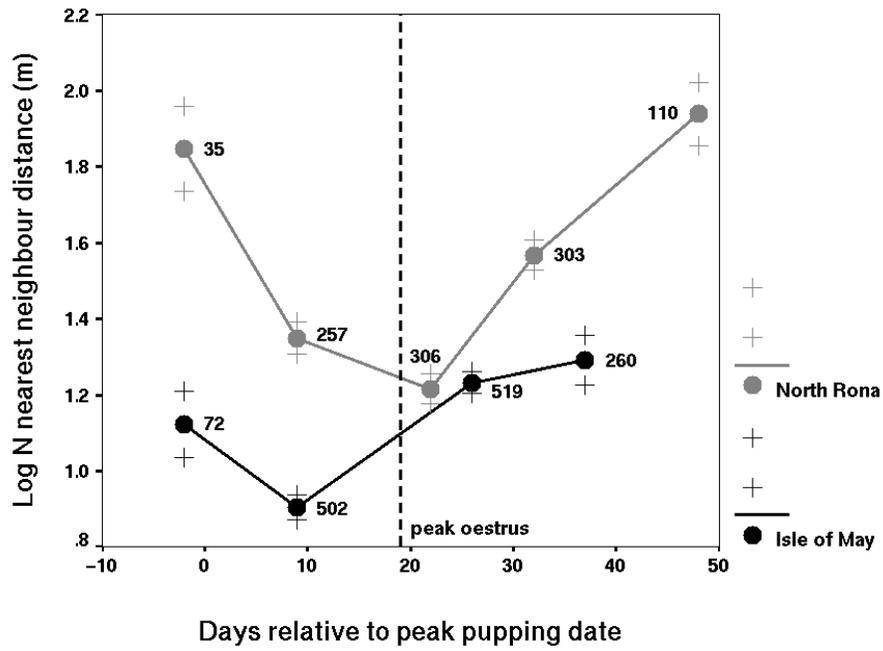
Site	Date	Mean	Standard error	No. of groups	Sex ratio
Isle of May	-2	2.15	0.21	8	1:10.29
	9	3.15	0.17	18	1:29.50
	26	2.41	0.14	36	1:14.83
	37	1.07	0.12	47	1:3.88
North Rona	-2	0.62	0.13	15	1:1.30
	9	1.37	0.14	40	1:4.96
	22	1.81	0.14	37	1:7.49
	32	1.87	0.11	42	1:7.07
	48	1.71	0.20	16	1:6.17

Figure legends:

Fig. 1. Plot of seasonal changes in mean natural log transformed nearest neighbour distances for breeding females at the Isle of May and North Rona in 1994. Crosses indicate standard errors. Note: date is expressed in days relative to peak pupping date.

Fig. 2. Seasonal changes in the estimated number of females in oestrous per day for the Isle of May and North Rona 1994. Date is expressed as number of days relative to peak pupping date.

Mean and S.E. Log N nearest neighbour distances
for breeding females at the Isle of May and North Rona



Estimated seasonal changes in the proportion of females in oestrus
at the Isle of May and North Rona

