# REPRODUCTIVE PERFORMANCE LINKS TO FINE SCALE SPATIAL PATTERNS OF FEMALE GREY SEAL RELATEDNESS.

Pomeroy, P.P.[1], Worthington Wilmer, J[2*], Amos W.[2] & Twiss, S.D.[3].

[1]Sea Mammal Research Unit, University of St. Andrews, Gatty Marine Laboratory, St. Andrews, Fife KY16 8LB Scotland, UK.

[2]Molecular Ecology Group, Dept. of Zoology, University of Cambridge, Downing St. Cambridge CB2 3EJ  UK.

[3]Spatial Ecology Group, University of Durham, Department of Biological Sciences, Science Laboratories, South Road, Durham DH1 3LE UK.

[*] Current address: Dept. of Biology, Boston University, 5 Cummington St, Boston, MA USA.

Corresponding author:            Patrick Pomeroy,
                                 Sea Mammal Research Unit

                                 Tel. +1334 462631
                                 Fax +1334 462632
                                 Email P.Pomeroy@smru.st-andrews.ac.uk

**Summary**

Fine scale spatial patterns of female relatedness throughout the established grey seal breeding colony of North Rona, Scotland, were investigated by accurate mapping and spatially explicit analyses of a large sample (n=262) of mothers using variation at 9 microsatellite DNA loci. Local spatial autocorrelation analyses identified locations where seals were more highly related to the colony than average. These locations were also areas where the more successful females bred, were occupied first during each breeding season, were centrally placed locations of preferred habitat types and are likely to be the locations which were the first to be colonized historically. Mothers occupying such sites achieved higher than average pup growth rates, suggesting a founder fitness benefit.

Keywords: Grey seals, relatedness, fitness, reproduction, spatial patterns, GIS, habitat quality, topography.

Running head: Spatial relatedness of female grey seals

# 1. Introduction

In many species, the identity, social status and relatedness of the interactants determine the likely outcome of behavioural encounters, which often have reproductive consequences (eg Chesser 1991, Dunbar 1988, Whitehead & Dufault 1999). The importance of this "social context" for individual breeding performance is most evident and widely studied in accessible species which form permanent, or semi-permanent, groups (Chesser 1991, 1998, Pope 1992, Pusey & Packer 1995). However, social context is also likely to be important for species that form short-lived aggregations. For example, breeding success may be influenced by an individual's location within a seasonal breeding aggregation and the time at which it arrives and leaves the aggregation. It is important therefore to consider the social structure of aggregations when examining individual success. The most tractable component of this social structure is the spatio-temporal dispersion of related individuals within an aggregation.

Studies of the relationship between associative behaviour and breeding success and more particularly, its long-term fitness consequences, in long-lived marine mammals pose particular problems because of the temporal and geographic scales required to document complete life histories for individual animals. Cetaceans are known to form matrilineal and fission-fusion groupings whose stability can vary over large time scales (Amos et al. 1993, Norris et al. 1994, Slooten et al. 1993, Wells et al. 1987, Whitehead et al. 1991). In contrast, many pinniped species form large, but short-lived, aggregations during the annual pupping and mating season, usually at a few colonies that offer limited space for breeding, and then disperse at sea for the remainder of the year (e.g. Baldi et al. 1996, Francis et al. 1991). In the U.K., adult grey seals (*Halichoerus grypus*) come ashore to breed in the autumn, forming aggregations of tens to thousands of animals. Males (Twiss et al. 1994) and females (Pomeroy et al. 1994) show a high degree of fidelity to particular breeding sites within a colony, and some females return to breed at their birth location (Pomeroy et al. 2000a). The function of such fidelity remains uncertain, but nevertheless presents the possibility of longer term stabilty in colony composition and social structure, with a potential for local aggregations of closely related individuals (Pomeroy et al. 2000a). Here, we used accurate mapping of seals within a Geographical Information System (GIS) to identify spatial patterns of genetic relatedness within a breeding colony of grey seals. The relationship of such patterns to habitat features was examined using a Digital Terrain model (DTM) of the same site to obtain topographic habitat measures for these locations. Lastly, we examined local variation in direct measures of breeding performance in a sub-sample of known females and their offspring from a long term study of grey seal reproductive success. The fitness returns from such patterns of heterogeneity are considered.

## 2. Materials and Methods

*Study site and colony history*

The grey seal colony on the island of North Rona (59 06' N, 05 50' W) was established prior to the 1880s and has been the subject of a study of reproductive behaviour for 40 years (Boyd & Laws, 1962). The main seal breeding area is the Fianuis peninsula, measuring 1.0x0.3 km, which is divided into Study Area, Fianuis South, and Fianuis North (Pomeroy et al. 1994). Approximately 95% of the 1200 pups produced in a typical year are born between 19 September and 29 October (Harwood et al. 1991, Hiby et al. 1996, SMRU unpublished).

*Seal breeding behaviour.*

Female grey seals become sexually mature aged 3-5 and their reproductive longevity can exceed 25 years (Hewer 1960, Pomeroy et al. 1999). Males become socially mature at around 8 years old, although some appear on the breeding colonies before this age, and have potential breeding spans of up to 15 years (Worthington Wilmer et al. 2000, Twiss & Pomeroy, unpublished data). Individual females spend 18-20 days ashore, during which time they each bear and suckle one pup, come into oestrus towards the end of lactation and are mated. Weaning occurs abruptly when the female returns to the sea (Hewer 1960). Each breeding colony offers pupping sites of varying suitability, but females exhibit preferences for particular habitat characteristics. These are low slope, low elevation and easy access to or from the sea (Pomeroy et al. 1994, Pomeroy et al. 2000b, Twiss et al. in press). Known adult females on North Rona return to within a median distance of 55m from their previous pupping sites, irrespective of the number of years between comparisons (Pomeroy et al. 1994); adult males show similar site fidelity (median distance = 53m, Twiss et al., 1994). Whilst some dispersal from breeding sites occurs (Coulson & Hickling 1960, Harwood, Anderson & Curry 1975, Pomeroy et al. 1994, Twiss pers. obs.) philopatry seems common, as indicated through resightings (Pomeroy et al. 2000a) and by differences in microsatellite allele frequencies between colonies (Allen et al. 1995). At colonies where seals breed inland, such as North Rona, mothers tend to remain at their birth location (median daily movement of mothers occurs within a 10m radius of their pupping sites, Pomeroy & Aust, unpublished data) thereby adding stability to the colony within a breeding season.

*Sampling and mapping.*

During the peak of the 1996 breeding season a remote biopsy punch was used to collect $2mm^2$ skin samples from 262 mothers located throughout Fianuis. This sample represented approximately 80% of

the females present in the Study Area at the time and 50% of the females present in Fianuis North (Fig. 2). Our sample comprised 25% of the females breeding on North Rona in 1996. All sampling occurred under HO licence and a prophylactic antibiotic (tetracycline) was applied to sampled animals. Samples stored in DMSO were frozen at -20°C until they were genotyped for 9 polymorphic microsatellites as described earlier (Allen et al. 1995, Worthington Wilmer et al. 1999). Relatedness values (R) between all pairs of females were calculated according to Queller & Goodnight (1989) using the program Kinship (Goodnight software, http://bioc.rice.edu/Keck2.0/labs/).

The location of each sampled female was recorded on detailed fine grain maps of the breeding colony. Maps incorporating a 10x10m grid were derived from digitised geo-rectified high resolution aerial photographs (Twiss et al. 2000a, in press). Location was summarised as the central x,y coordinate of a specific 10m grid cell, allowing calculation of Euclidean distances between the centres of any pair of grid cells containing sampled females. Seals were sampled in 126 grid cells from Fianuis North to Study Area representing the full range of topographies used by breeding female seals at this colony (Boyd & Laws 1962; Pomeroy *et al*. 1994). These same maps were used to make daily records of the location of every seal, identified by sex and age. Estimates of the density of adult females in each 10m grid cell were derived from these daily maps of seals' locations at the peak of the breeding season when sampling occurred.

The locations of all sampled and mapped females were stored in a Geographical Information System (GIS) together with a sub-meter resolution Digital Terrain Model (DTM) generated from the same aerial photos of the colony (Mills et al. 1997, Twiss et al. 2000a) so that local female density and topographic habitat descriptors could be included in analyses of factors likely to be important in determining local indices of relatedness. Each 10m grid cell was characterised by the median elevation and slope of its 2500 constituent 0.2m sub-cells. These values were used to generate cost-surface models which provide, for each location, an index describing the relative distances from the location to points of access from the sea and to pools of water in the colony, whilst accounting for the difficulty of terrain traversed in reaching water (Twiss et al. 2000b, in press). Sampling effort was calculated as the proportion of females present in each 10m grid cell that had been sampled.

*Testing for local kin aggregations – are neighbours highly related?*
The aggregation of seals into two breeding areas separated by 400m (Study Area and Fianuis North) created a bimodal distribution of distances between sampled animals (d), making it difficult to identify

patterns of relatedness.  To correct for this, we generated a joint distribution of R and d in which the continuous distribution of R from -1 to +1 was split into 20 x 0.1 bins and d, ranging from 0-800m, was split into 40 x 20m bins. Frequencies of observations for discrete R bins within each distance category were standardised for the total number of observations over that specific distance category. These standardised frequencies (in effect a proxy for probability) were then displayed as the corrected joint distribution for evidence of distance effects on R.

*Examining the spatial pattern of relatedness using Local Spatial Autocorrelation*

This approach provides an index which describes the relative shift in local mean values compared to the global mean: that is, it identifies locations where local data values tend to be higher, or lower than the global average.  Here, our aim was to produce a map indicating  where local groups of seals are more, or less, related to the colony as a whole when compared to our global (sample) average.   Local spatial autocorrelation  (Gi*(d)) statistics (Getis & Ord 1992, Ord & Getis 1995, Sokal et al. 1998) were calculated to identify locations of statistically significant nonstationarity ('hotspots') in the mapped patterns of relatedness. At each sampled location, the average of all dyadic relatedness values from females within a specified radius (10, 20, 30, 40 and 50m) of the focal sampling point was compared to the average relatedness of all sampled females.  A positive Gi* statistic for a location indicates clustering of high R values (most highly related seals) within the specified radius of that location with respect to the global mean, while negative Gi* statistics indicate clustering of low values (most unrelated seals). Standardized normal values for the local spatial autocorrelations were calculated as ZGi*(d). The pattern of occurrence of locations with high or low ZGi*(d) statistics was of particular interest. ZGi*(d) values were categorised using a $\pm$ 1sd cutoff to define locations with high, medium or low ZGi*(d) values, enabling sampling locations to be mapped and visualised according to their relatedness categories. Local spatial autocorrelation calculations were conducted using the Rookcase Visual Basic routine (Sawada 1999).

*The spatial pattern of relatedness and habitat characteristics*

We investigated the ability of elevation, slope, distance to nearest access, distance to nearest pools, female density and sampling intensity to account for variation in uncategorised, continuous ZGi*(d) values at each location in the Study Area using stepwise multiple regression procedures.  Variables were retained at a critical level of p=0.05.

*Reproductive performance and patterns of relatedness*

Intra-annual measures of reproductive performance for known seals were compared at the sampling

locations categorized by ZGi*(d) values.  Contrasts were between high ZGi*(d) locations (>1SD of the Zgi*(30m) distribution) and all other locations.  Maternal mass loss rate, estimated from the difference in mass of mothers near the start and end of the lactation period was used as an index of maternal performance (Pomeroy et al. 1999).  The growth rate of pups (kg/d), estimated from the difference in mass of pups near the start and end of the lactation period, taking account of mother's identity, was used as an index of breeding performance for mothers and their pups weighed in 1996 and 1997.   For the purposes of this analysis, locations sampled in 1997 were assumed to have the same relatedness attributes as they had in 1996.

All statistical procedures were carried out in SPSS 8 & 9 or Minitab 11.

## 3. Results

*Testing for local kin aggregations – are neighbours highly related?*
Individual relatedness values ranged from -0.62 to +0.68.  The overall average level of relatedness between dyads in our sample was 0.00 $\forall$ 0.18 (s.d.,  n=262, 33826 comparisons).  Euclidean distances separating dyads ranged from 0 to 799.9m.  There was no evidence of a simple relationship between relatedness values and the distance separating dyads, after the effects of the bimodal distance distribution between sampling locations had been taken into account (Fig. 1).  However this analysis referred only to the distance separating two females, without any simultaneous consideration of how dyad members were related spatially to other sampled seals.

*Examining the spatial pattern of relatedness using Local Spatial Autocorrelation*
Local spatial autocorrelation analysis indicated that there were locations where on average, individuals within a radius of 30m had higher than average relatedness to all others in the colony (high positive ZGi* statistics, Fig 2).   Such locations also tended to be aggregated at the centres of seal groupings (Fig.2).  Aggregations of locations expressing high ZGi* values became less evident at scales of 20m to 10m and at 50m.  Thus locations with higher than average relatedness to the colony as a whole were most clustered when the radii of inclusion were 30m or 40m.

*The spatial pattern of relatedness and habitat characteristics*
Our null hypothesis was that there would be no relationship between local habitat quality and the average relatedness of seals at a location in comparison to the colony as a whole (ZGi*).  Regression models of ZGi* values and the habitat descriptors for these locations indicated "distance to access" as

an important explanatory variable (Table 1). These relationships were best described by a cubic model for the spatial scales of 30m, 40m and 50m (Table 1) and suggested that ZGi* increased up to "distance to access" values of approximately 80 and then declined with increasing distance to access, in an index ranging from 0 to 300 (where 0 = the access point where it meets the sea, and 300 = the maximum access value obtained inland). Elevation was also a significant explanatory variable at each scale considered, but is highly correlated (Spearman's rho 0.96, n= 86, p<0.001) with distance to access at these locations and, in this context at least, has less obvious biological meaning than distance to sea. Slope featured as a barely significant variable at the 50m scale. No other potential factors, including local animal density and sampling intensity, were significant. These results imply that the average relatedness of seals at a location in comparison to the colony as a whole was greatest at specific low-lying locations that are some optimum distance from access to the sea on this colony.

*Reproductive performance and patterns of relatedness*

There were differences in individual reproductive performance data from known seals according to their ZGi*(30m) category. Although maternal postpartum masses and parturition dates were not significantly different, maternal mass loss rates were greater in locations of higher than average relatedness to the colony as a whole compared to other locations (Table 2). Growth rates of pups tended in a similar direction. There was no difference in growth rate of pups according to their sex (males 2.04±0.50 (s.d.), females 1.88±0.40, t=1.005, d.f.=37, p>0.3). The efficiency of mass transfer for mothers (estimated by pup daily growth rate / mothers daily mass loss) was the same in the two area categories. Growth rates of pups were greater in locations of higher than average relatedness to the colony as a whole compared to other locations when maternal mass loss rate and mother's identity were taken into account in a General Linear Model (Table 3). The difference in growth rates of pups between area categories remained when only the few 1996 data were examined, (2.59± 0.30 (s.d.), 2.04±0.36, t = 2.48, d.f. = 15, p=0.026). There was no relationship between the ages of weighed mothers and relatedness at their location, but the small aged sample (n=18) was biased towards older females, while the larger relatedness sample (n=262) should be representative of the female age structure in the colony.

## 4. Discussion

We found that: (i) locations where on average female grey seals were more related to the colony were aggregated at scales of 30-40m within the North Rona colony; (ii) such locations occurred in areas

close to the main access points to the colony, but away from the access points themselves; (iii) pups in areas of higher relatedness had higher growth rates than those elsewhere, but these could not be explained by differences in maternal size or efficiency. While repeated, spatially accurate breeding site fidelity and philopatry would be expected to generate local clumps of closely related kin (Pomeroy et al. 2000a), the fine-scale genetic structuring within the breeding colony, uncovered using this microsatellite approach, does not appear to be based solely on local direct kin association, as dyads of females at these locations did not show higher relatedness than in colony-wide dyadic comparisons (Fig.1). However, females occupying central breeding locations contribute more to the colony than females elsewhere, probably through habitat-related fitness benefits. Females in central areas showed better intra-seasonal reproductive performance in producing bigger, faster-growing pups that are likely to have higher than average survival (Hall et al. in press). This self-reinforcing feedback allows certain genetic strains to become prevalent in the colony, as revealed by our snapshot of genetic make-up of the colony (Fig. 2).

Locations containing seals with higher than average relatedness to the colony as a whole occurred in core areas of the N. Rona colony. These locations occur close to access points, but avoid the busy access points themselves which act as thoroughfares for animals arriving at or departing from the colony (Anderson et al. 1975, Twiss et al. in press). Other proximate benefits for individuals occupying these prime locations include access to predictable resources. Breeding females require relatively flat terrain with ready access to water (Twiss et al. 2000b, in press)). At North Rona there is an excess of suitably flat terrain (hence no effect of slope), but access to water can be more limiting. Availability of water is known to be an important factor in pupping site selection and standing pools are a feature of areas which are occupied first (Pomeroy et al. 1994, Twiss et al. 2000b). Females that breed early are larger than average, produce bigger pups and have fewer pupping failures than later breeding females (Pomeroy et al. 1999). Mothers forming the two subsamples of weighed animals in this analysis had similar pupping dates and partum masses, so the differences in growth rates of their pups and maternal rates of mass loss according to relatedness area category could not be attributed simply to either maternal size or to N. Rona's temporal cline in maternal size (Pomeroy et al. 1999). As the average efficiency of mass transfer was similar for the two area categories, the higher pup growth rates and maternal mass loss rates recorded in the areas of higher than average relatedness to the colony as a whole were likely the result of greater suckling rates. Maternal quality may vary enough to account for these differences (Table 3) as documented elsewhere (Mellish et al. 1999, Pomeroy et al. 1999), but it is also possible that harassment of mothers by transient males away from areas containing dominant males, particularly in the later part of the season, could contribute to the

lower growth rates recorded there (Boness et al. 1995).

In other species where mothers can affect daughter quality, for example, by passing on social status or high quality territory, variation in female reproductive success is substantial and may even exceed that of males (Hausfater et al. 1982, Leimar 1996). Female grey seals show substantial variance not only in the number of pups they raise successfully, but in the size of pups they produce (Pomeroy et al. 1999). Our analyses indicate the locations where the more successful mothers breed. Furthermore, these locations cluster in areas which are defined by unchanging topography and therefore are likely to be used consistently by the higher quality mothers. This suggests that locations may be important predictors of mate quality for males. Socially dominant males tend to occupy central positions (Twiss et al. 1998). In a moderately polygynous species such as the grey seal, males may compete for prime breeding locations, which on average will have the highest quality females.

At present it is not possible to distinguish between cause and effect for locality and breeding success. The core areas occupied first during each breeding season are likely to be the areas which were the first to be colonized historically (Anderson et al. 1975, Pomeroy et al. 1994, Pomeroy et al. 2000b, Twiss et al. 2000b). Here, we have demonstrated for the first time that mothers breeding in central parts of the colony are not only more successful in rearing pups within years, but are also the current representatives of the more prevalent genotypes in the colony. These results suggest that as long as the relationship between female quality, reproductive performance and habitat quality is robust, long term spatial genetic structuring of the N. Rona colony should persist.

While this approach has demonstrated non-random distribution of relatedness among breeding female grey seals at North Rona within a season, the inter-annual stability of this pattern is unknown. Colony social structure elsewhere may be different and it remains to be seen whether similar colony structure occurs where topographic variation and/or site-fidelity and philopatry is minimal (e.g. Boness & James 1979). However, the ability to view the behaviour of individuals against a fine spatial scale "genetic map" of a breeding colony provides a clearer view of the factors which may influence short term individual choices and their ultimate fitness consequences. Grey seal breeding colonies represent temporary aggregations, yet social structure is apparent. Even amongst temporary, or at least semi-permanent, aggregations social structure is likely to be widespread. This is likely to be the case where (i) individuals vary in competitive ability, (ii) resources vary in quality and (iii) variation in resource quality within groups remains constant over time. This last feature is not restricted to physical attributes such as topography: social factors such as relative position within a mobile group

may similarly constitute a variable resource. These features are likely to be common amongst temporary aggregations across species. Finally, as we have shown for grey seals, such structuring can have fitness consequences.

## References:

Allen, P. J., W. Amos, P. P. Pomeroy, & S. D. Twiss. 1995. Microsatellite variation in grey seals *Halichoerus grypus* shows evidence of genetic differentiation between two British breeding colonies. *Molecular Ecology*, **4,**653-662.

Amos, W., C. Schlötterer, & D. Tautz. 1993. Social structure of pilot whales revealed by analytical DNA typing. *Science* **260**, 670-672.

Anderson, S. S., R. W. Burton, & C. F. Summers. 1975. Behaviour of grey seals *Halichoerus grypus* during a breeding season at North Rona. *Journal of Zoology*, **177,**179-195.

Baldi, R., Campagna, C., Pedraza, S. & LeBoeuf, B.J. 1996. Social effects of space availability on the breeding behaviour of elephant seals in Patagonia. *Animal Behaviour* **51**, 717-724.

Boyd, J. M., & R. M. Laws. 1962. Observations on the grey seal (*Halichoerus grypus*) at North Rona in 1960. *Proceedings of the Zoological Society of London*, **164,** 469-512.

Boness , D.J. & H. James. 1979. The reproductive behaviour of the grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. *Journal of Zoology*, **188,** 477-500.

Boness, D.J., D. Bowen & S.J. Iverson. 1995. Does male harassment of females contribute to reproductive synchrony in the grey seal by affecting maternal performance? *Behavioural Ecology and Sociobiology* **36,** 1-10.

Chesser, R.K. 1991. Gene diversity and female philopatry. *Genetics* **127**: 437-447.

Chesser, R.K. 1998. Relativity of behavioural interactions in socially structured populations. *Journal of Mammalogy* **79**(3):713-724.

Coulson, J. C., & G. Hickling. 1960. The Grey seals of the Farne Islands 1958-1959. *Transactions of the Natural History Society of Northumberland*, **13,**151-178.

Dunbar R.I.M. 1988. *Primate social systems*. Comstock, Ithaca.

Francis, J.M. & Boness, D.J. 1991. The effect of thermoregulatory behaviour on the mating system of the Juan Fernandez fur seal, *Arctocephalus philippi*. *Behaviour* **42**, 104-126.

Getis, A. & J.K. Ord. 1992. The analysis of spatial association by use of distance statistics. *Geographical Analysis* **24**(3), 189-206.

Hall, A. J., B.J. McConnell & R.J. Barker. In press. Factors affecting first-year survival in grey seals and their implications for life history strategy. *Journal of Animal Ecology*.

Harwood, J., L. Hiby, D. Thompson, & A. Ward. 1991. Seal stocks in Great Britain. Surveys conducted between 1986 and 1989. *NERC News*, January,**11-15.

Harwood, J., S.S. Anderson & M.G. Curry. 1975. Branded grey seals at the Monach Isles, Outer Hebrides. *Journal of Zoology* **180**: 506-508.

Hausfater, G., J. Altman, S. Altman. 1982. Long-term consistency of dominance relations among female baboons (*Papio cynocephalus*). *Science* 217: 752-755.

Hewer, H. R. 1960. Behaviour of the grey seal (*Halichoerus grypus* Fab.) in the breeding season. *Mammalia*, **24,**400-421.

Hiby, A. R., C. D. Duck, D. Thompson, A. J. Hall, & J. Harwood. 1996. Seal Stocks in Great Britain. *NERC News*, (January)20-22.

Leimar, O. 1996. Life-history analysis of the Trivers and Willard sex-ratio problem. *Behav. Ecol.* **8**, 395-400.

Mellish, J.E., S. Iverson & D. Bowen. 1999. Variation in milk production and lactation performance in grey seals and consequences for pup growth and weaning characteristics. *Physiological and Biochemical Zoology* **72**(6), 677-690.

Mills, J. P., I. Newton & S.D. Twiss. 1997. Photogrammetry from archived digital imagery for seal monitoring. *Photogrammetric Record* **15**(89): 715-724.

Norris K.S., B. Wηrsig, R.S. Wells, & M. Wηrsig. 1994. *The Hawaiian spinner dolphin*. Univ. of California Press, Los Angeles.

Ord, J.K. & A. Getis. 1995. Local spatial autocorrelation statistics: distributional issues and an application. *Geographical Analysis* **27**(4), 287-305.

Pomeroy, P. P., S. S. Anderson, S. D. Twiss, & B. J. McConnell. 1994. Dispersion and site fidelity of breeding female grey seals (*Halichoerus grypus*) on North Rona, Scotland. *Journal of Zoology*, **233,** 429-448.

Pomeroy, P. P., M. A. Fedak, S. S. Anderson, & P. Rothery. 1999. Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. *Journal of Animal Ecology*, **68,** 235-253.

Pomeroy, P. P., S. D. Twiss, & P. Redman. 2000a. Philopatry, site fidelity and local kin associations within grey seal breeding colonies. *Ethology* **106**, 899-919.

Pomeroy, P. P., S. D. Twiss, & C.D. Duck. 2000b. Expansion of a grey seal (*Halichoerus grypus*) breeding colony: changes in pupping site use at the Isle of May, Scotland. *Journal of Zoology*, **250,** 1-12.

Pope, T.R. 1992. The influence of dispersal patterns and mating system on genetic differentiation within and between populations of the red howler monkey (*Alouatta seniculus*). *Evolution* **46**, 1112-1128,

Pusey, A.E. & Packer, C. 1995. The ecology of relationships. In *Behavioural ecology* 4th edition (ed. J.Krebs & N. B. Davies) pp 254-283. Oxford: Blackwell Scientific Publications.

Queller, D. C. & Goodnight, K. F. 1989 Estimating relatedness using genetic markers. *Evolution* **43**, 258-275.

Sawada, M. 1999. Rookcase: An Excel 97/2000 Visual Basic (VB) Add-In for exploring global and local spatial autocorrelation. *Bulletin of the Ecological Society of America*, **80**(4), 231-234.

Slooten, E., S.M. Dawson & H. Whitehead. 1993. Associations among photographically identified Hector's dolphins. *Can. J. Zool.* **71**, 2311-2318.

Sokal, R.R., N.L. Oden & B.A. Thompson. 1998. Local spatial autocorrelation in a biological variables. *Biological Journal of the Linnean Society* **65**, 41-62.

Twiss, S. D., S.S. Anderson & P. Monaghan. 1998. Limited intra-specific variation in male grey seal (*Halichoerus grypus*) dominance relationships in relation to variation in male mating success and female availability. *Journal of Zoology* **246**, 259-267.

Twiss, S. D., P. P. Pomeroy, C. J. Thomas, & J. P. Mills. 2000a. Remote estimation of grey seal length, width and body mass from aerial photography. *Photogrammetric Engineering and Remote Sensing* **66**(7) 859-866.

Twiss, S. D., A. Caudron, P. P. Pomeroy, C. J. Thomas, & J. P. Mills. 2000b. Fine scale topographical correlates of behavioural investment in offspring by female grey seals. *Animal Behaviour*. **59**(2), 327-338

Twiss, S. D., P. P. Pomeroy, & S. S. Anderson. 1994. Dispersion and site fidelity of breeding male grey seals (*Halichoerus grypus*) on North Rona, Scotland. *Journal of Zoology*, **233,**683-693.

Twiss S.D., C.J. Thomas & P.P. Pomeroy. (in press). Topographic spatial characterisation of grey seal *Halichoerus grypus* breeding habitat at a seal's perceptual spatial grain. *Ecography*

Wells, R.S., M.D. Scott & A.B. Irvine. 1987. The social structure of free ranging dolphins. In *Current Mammalogy* (ed. H.H. Genoways) Vol. 1, pp 247-305. Plenum, New York.

Whitehead, H., S. Waters & T. Lyrholm. 1991. Social organization in female sperm whales and their offspring: Constant companions and casual acquaintances. *Behavioural Ecology and Sociobiology* **29**, 385-389.

Whitehead, H. & S. Dufault. 1999. Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. *Advances in the Study of Behaviour* **28**, 33-73.

Worthington Wilmer, J.,  P. Allen, P.P. Pomeroy, S.D. Twiss, & W. Amos.  1999. Where have all the fathers gone? An extensive microsatellite analysis of paternity in the grey seal (*Halichoerus grypus*). *Molecular Ecology* 8, 1417-1429.

Worthington Wilmer, J., A.J. Overall, P.P. Pomeroy, S.D. Twiss, & W. Amos. 2000. Patterns of paternal relatedness in British grey seal colonies. *Molecular Ecology* **9**: 283-292.

Figure legends.

Figure 1.  Surface plot of standardised frequencies of occurrence for the joint distribution of relatedness, R and distance (m) separating pairs of  female grey seals sampled on North Rona in 1996.

Figure 2.  Categorised local spatial autocorrelation ZGi*(d) statistics for locations where seals were sampled in 1996, displayed on a surface of 'cost-distance to access' map of Fianuis, North Rona. Note that sampled locations are indicative of seal distribution on Fianuis.  A positive Gi* statistic indicates clustering of high relatedness (R) values of females within a radius of (d)m from a location with respect to the global mean, while negative Gi* statistics indicate clustering of low values. The radius (d) for this plot was 30m.  Standardised Gi*(d) values were categorised for visualisation using a 1 S.D. cutoff, such that locations with similarly high, average and low R values compared to the colony as a whole are represented by white triangles, grey circles and black triangles respectively.
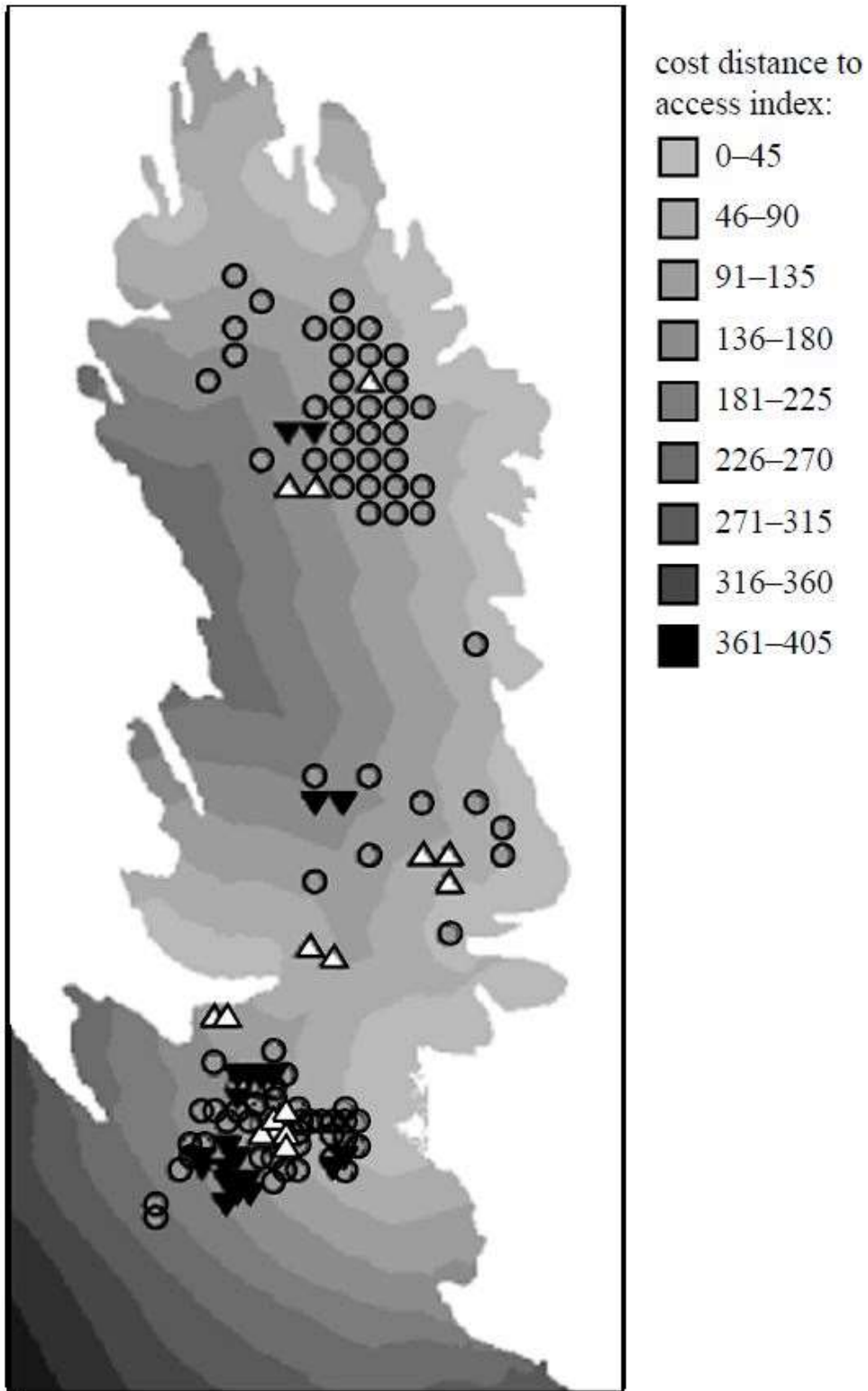
Figure 1

cost distance to
access index:

☐ 0–45
☐ 46–90
☐ 91–135
☐ 136–180
☐ 181–225
☐ 226–270
☐ 271–315
☐ 316–360
■ 361–405
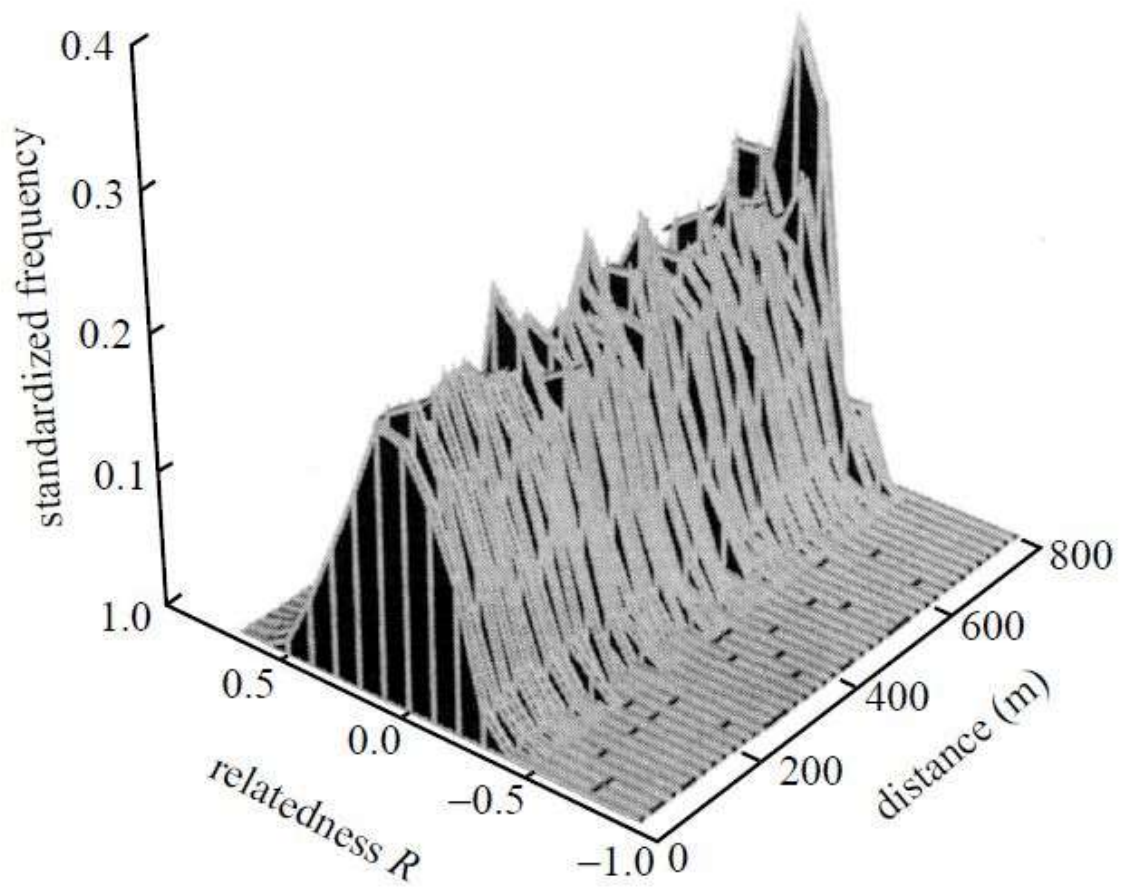
Figure 2

Table 1.  Regression models of variation in local spatial autocorrelation statistics $ZGi^*(d)$ for relatedness of female grey seals at locations on North Rona, 1996.  Linear, quadratic and cubic models of the relationship between $ZGi^*$ and distance to nearest access (DTA, Twiss et al. 2000) as the single important explanatory variable were compared. There was no significant relationship between $ZGi^*(d)$ and DTA at 10 or 20m scales for linear, quadratic or cubic models.  For the 30, 40 and 50m cases, the cubic model showed a significant reduction in the error sum of squares compared to the quadratic and linear models. Elevation was also a significant predictor variable, but was highly correlated with distance to access. Slope, female density at time of sampling and sampling intensity were not significant.

| $ZGi^*(d)$ radius | Model: cubic, n=128 locations | $R^2$ | d.f. | F | Signif. |
|---|---|---|---|---|---|
| 10m | | 0.044 | 79 | 1.2 | 0.307 |
| 20m | | 0.081 | 79 | 2.32 | 0.081 |
| 30m | $ZGi^* = 0.571 \times DTA - 0.0056 \times DTA^2 + 0.000015 \times DTA^3 - 15.15$ | 0.273 | 79 | 9.9 | <0.001 |
| 40m | $ZGi^* = 0.511 \times DTA - 0.0048 \times DTA^2 + 0.000012 \times DTA^3 - 14.34$ | 0.475 | 79 | 23.8 | <0.001 |
| 50m | $ZGi^* = 0.175 \times DTA - 0.0018 \times DTA^2 + 0.000004 \times DTA^3 - 3.70$ | 0.474 | 79 | 23.8 | <0.001 |

Table 2. Birth date, mass and mass change data for mothers and pups on North Rona according to pupping location, categorised as either: High Zgi* - locations with higher than average (>1S.D. of the ZGi* distribution at 30m scale) relatedness to the colony as a whole; or Other - all other locations where seals were sampled.   Comparisons among groups use 2-tailed t-tests.

| Variable | Location relatedness category | N | Mean | Std. Deviation | Std. Error Mean | t | df | Sig. (2-tailed) |
|---|---|---|---|---|---|---|---|---|
| Birth date (1= 1 Sept) | High  ZGi* | 8 | 36.1 | 6.5 | 2.30 | -0.952 | 35 | 0.348 |
| | Other | 29 | 38.7 | 6.7 | 1.24 | | | |
| Maternal post partum mass (kg) | High  ZGi* | 8 | 198.0 | 16.3 | 5.76 | 0.193 | 29 | 0.848 |
| | Other | 23 | 196.7 | 17.0 | 3.54 | | | |
| Maternal mass loss rate (kg/d) | High  ZGi* | 7 | 4.45 | 0.48 | 0.18 | 2.130 | 28 | 0.042 |
| | Other | 23 | 3.85 | 0.69 | 0.14 | | | |
| Pup growth rate (kg/d) | High  ZGi* | 7 | 2.28 | 0.43 | 0.164 | 1.905 | 28 | 0.067 |
| | Other | 23 | 1.95 | 0.39 | 0.080 | | | |
| Mass transfer efficiency (pup growth rate/ maternal mass loss rate) | High  ZGi* | 7 | 0.509 | 0.050 | 0.019 | 0.142 | 28 | 0.888 |
| | Other | 23 | 0.506 | 0.038 | 0.008 | | | |

Table 3.  General linear model of pup growth rate (kg/d) according to maternal mass loss rate (MMLR, kg/d),  ZGi* location category (locations with higher than average (>1S.D. of the ZGi* distribution at 30m scale) relatedness to the colony as a whole, or other) and mother's identity for grey seals at North Rona in 1996 and 1997.   Adjusted $r^2$ = 0.958.   Birth date (F=0.041, p>0.8) and the interaction term between mother's identity and ZGi* location category (F=1.35, p>0.35) were dropped from the model.

| source | Sums of squares | Degrees of freedom | Mean square | F | Significance |
|---|---|---|---|---|---|
| Model | 4.919 | 22 | 0.224 | 31.265 | <0.001 |
| intercept | 0.042 | 1 | 0.042 | 5.878 | 0.046 |
| MMLR | 0.623 | 1 | 0.623 | 87.05 | <0.001 |
| ZGi* location category | 0.049 | 1 | 0.049 | 6.870 | 0.034 |
| Mother's identity | 0.661 | 20 | 0.033 | 4.622 | 0.023 |
| Error | 0.05006 | 7 | 0.00715 | | |
| Total | 128.456 | 30 | | | |
| Corrected total | 4.969 | 29 | | | |