

Reproductive performance links to fine-scale spatial patterns of female grey seal relatedness

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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 nine 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 were 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; habitat quality

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 (e.g. Dunbar 1988; Chesser 1991; Whitehead & Dufault 1999). The importance of this 'social context' for individual breeding performance is most evident and widely studied in accessible species that 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 therefore important 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 for documenting complete life histories for individual animals. Cetaceans are known to form matrilineal and fission–fusion groupings, the stability of which can vary over large time-scales (Wells *et al.* 1987; Whitehead *et al.* 1991; Amos *et al.* 1993; Slooten *et al.* 1993; Norris *et al.* 1994). 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. Francis & Boness 1991; Baldi *et al.* 1996). In the UK, 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 stability 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 in order to obtain topographic habitat measures for these locations. Lastly, we examined local variation in direct measures of breeding performance in a subsample 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. MATERIAL AND METHODS

(a) 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 1.0 km × 0.3 km, which is divided into the 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; Sea Mammal Research Unit, University of St Andrews, unpublished data).

(b) Seal breeding behaviour

Female grey seals become sexually mature at age three to five years, and their reproductive longevity can exceed 25 years

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(Hewer 1960; Pomeroy *et al.* 1999). Males become socially mature at around eight years old, although some appear on the breeding colonies before this age and have potential breeding spans of up to 15 years (WorthingtonWilmer *et al.* 2000; S. D. Twiss and P. P. 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, 2000b; Twiss *et al.* 2001). Known adult females on North Rona return to within a median distance of 55 m 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 = 53 m) (Twiss *et al.* 1994). Whilst some dispersal from breeding sites occurs (Coulson & Hickling 1960; Harwood *et al.* 1975; Pomeroy *et al.* 1994; S. D. Twiss, personal observation) 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 (the median daily movement of mothers occurs within a 10 m radius of their pupping sites) (P. P. Pomeroy and J. Aust, unpublished data), thereby adding stability to the colony within a breeding season.

(c) *Sampling and mapping*

During the peak of the 1996 breeding season, a remote biopsy punch was used to collect 2 mm² skin samples from 262 mothers located throughout Fianuis. This sample represented *ca.* 80% of the females present in the Study Area at the time and 50% of the females present in Fianuis North. Our sample comprised 25% of the females breeding on North Rona in 1996. All sampling occurred under Home Office licence and a prophylactic antibiotic (tetracycline) was applied to sampled animals. Samples were stored in dimethylsulphoxide and frozen at –20 °C until they were genotyped for nine polymorphic microsatellites as described earlier (Allen *et al.* 1995; WorthingtonWilmer *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 female sampled was recorded on detailed fine grain maps of the breeding colony. Maps incorporating a 10 m × 10 m grid were derived from digitized, georectified, high-resolution aerial photographs (Twiss *et al.* 2000a, 2001). Location was summarized as the central x, y coordinate of a specific 10 m 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 the 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 as identified by sex and age. Estimates of the density of adult females in each 10 m 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 GIS together with a sub-metre resolution 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 10 m grid cell was characterized by the median elevation and slope of its 2500 constituent 0.2 m subcells. These values were used to generate cost–surface models that provide an index for each location, 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, 2001). Sampling effort was calculated as the proportion of females present in each 10 m grid cell that had been sampled.

(d) *Testing for local kin aggregations: are neighbours highly related?*

The aggregation of seals into two breeding areas separated by 400 m (the study area and Fianuis North) created a bimodal distribution of distances between sampled animals (d) making it difficult to identify patterns of relatedness. In order 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 20×0.1 bins and d , which ranged from 0 to 800 m, was split into 40×20 m bins. The frequencies of observations for discrete R bins within each distance category were standardized for the total number of observations over that specific distance category. These standardized frequencies (in effect a proxy for probability) were then displayed as the corrected joint distribution for evidence of distance effects on R .

(e) *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 similarly higher or similarly lower than the global average. Here, our aim was to produce a map indicating where local groups of seals were more related or less related to the colony as a whole when compared to our global (sample) average. Local spatial autocorrelation ($G_i^*(d)$) statistics (Getis & Ord 1992; Ord & Getis 1995; Sokal *et al.* 1998) were calculated in order to identify locations of statistically significant non-stationarity ('hot spots') in the mapped patterns of relatedness. At each location sampled, the average of all dyadic relatedness values from females within a specified radius (10, 20, 30, 40 and 50 m) of the focal sampling point was compared to the average relatedness of all females sampled. A positive G_i^* 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 G_i^* statistics indicate clustering of low values (most unrelated seals). Standardized normal values for the local spatial autocorrelations were calculated as $ZG_i^*(d)$. The pattern of occurrence of locations with high or low $ZG_i^*(d)$ statistics was of particular interest. $ZG_i^*(d)$ -values were categorized using a ± 1 s.d. cut-off in order to define locations with high, medium or low $ZG_i^*(d)$ -values, enabling sampling locations to be mapped and visualized according to their relatedness categories. Local spatial autocorrelation calculations were conducted using the Rookcase Visual Basic routine (Sawada 1999).

(f) *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

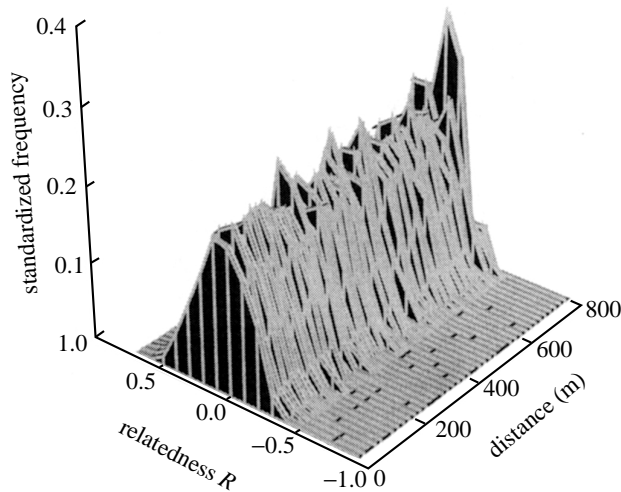


Figure 1. Surface plot of standardized frequencies of occurrence for the joint distribution of relatedness R and distance (m) separating pairs of female grey seals sampled on North Rona in 1996.

sampling intensity to account for variation in uncategorized, continuous $\chi_{Gi^*}(d)$ -values at each location in the study area using stepwise multiple regression procedures. Variables were retained at a critical level of $p = 0.05$.

(g) *Reproductive performance and patterns of relatedness*

Intra-annual measures of reproductive performance for known seals were compared at the sampling locations categorized by $\chi_{Gi^*}(d)$ -values. Contrasts were between high $\chi_{Gi^*}(d)$ locations (> 1 s.d. of the $\chi_{Gi^*}(30\text{ m})$ distribution) and all other locations. Maternal mass loss rate, as estimated from the difference in the 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 day^{-1}), as estimated from the difference in the mass of pups near the start and end of the lactation period, taking account of the 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 9 or Minitab 10.5.

3. RESULTS

(a) *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 (\pm s.d.) between dyads in our sample was 0.00 ± 0.18 ($n = 262$ with 33 826 comparisons). The Euclidean distances separating dyads ranged from 0 to 799.9 m. There was no evidence of a simple relationship between the relatedness values and the distance separating dyads after the effects of the bimodal distance distribution between sampling locations had been taken into account (figure 1). However, this analysis only referred to the distance separating two females, without any simultaneous consideration

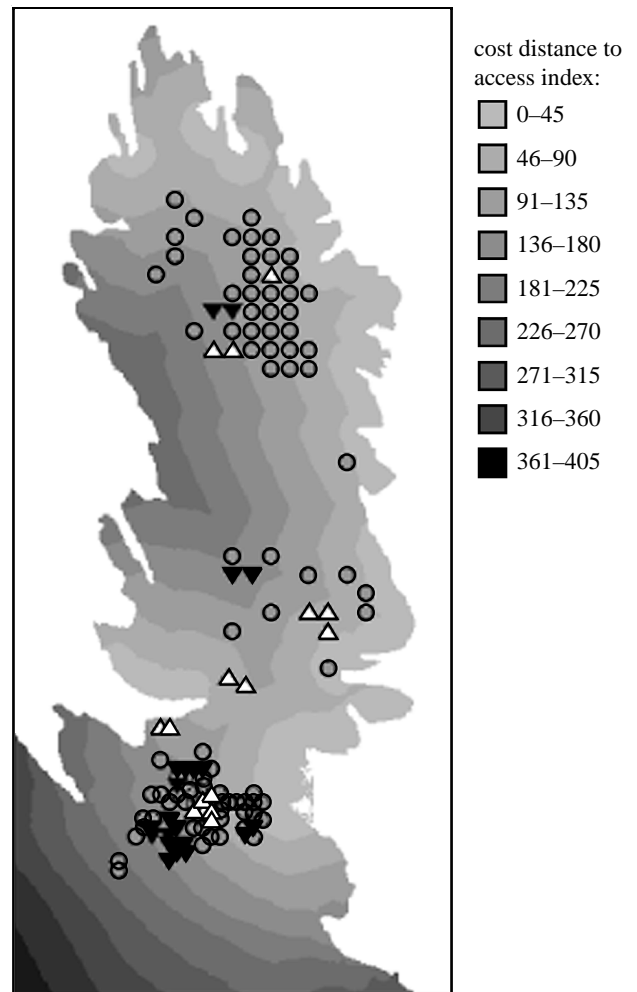


Figure 2. Categorized local spatial autocorrelation $\chi_{Gi^*}(d)$ statistics for locations where seals were sampled in 1996 displayed on a surface of 'cost-distance to access' map of Fianuis, North Rona. Note that sampled locations are indicative of the seal distribution on Fianuis. A positive G_i^* 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 G_i^* statistics indicate clustering of low values. The radius (d) for this plot was 30 m. Standardized $G_i^*(d)$ -values were categorized for visualization using a 1 s.d. cut-off 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.

of how dyad members were spatially related to other sampled seals.

(b) *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 30 m had higher than average relatedness to all others in the colony (high positive χ_{Gi^*} statistics) (figure 2). Such locations also tended to be aggregated at the centres of seal groupings (figure 2). Aggregations of locations expressing high χ_{Gi^*} -values became less evident at scales of 10, 20 and at 50 m. Thus, locations with higher than average relatedness to the

Table 1. Regression models of variation in local spatial autocorrelation statistics ζGi^* (d) for relatedness of female grey seals at locations on North Rona, 1996

(Linear, quadratic and cubic models of the relationship between ζGi^* and distance to nearest access (DTA) (Twiss *et al.* 2000*b*) as the single important explanatory variables were compared. There was no significant relationship between ζGi^* and distance to nearest access at the 10 or 20 m scales for the linear, quadratic or cubic models. The cubic model showed a significant reduction in the error sum of squares compared to the quadratic and linear models for the 30, 40 and 50 m cases. Elevation was also a significant predictor variable, but was highly correlated with distance to nearest access. Slope, female density at time of sampling and sampling intensity were not significant.)

ζGi^* (m)	cubic model ($n = 128$ locations)	R^2	d.f.	F	significance
10	—	0.044	79	1.20	0.307
20	—	0.081	79	2.32	0.081
30	$\zeta Gi^* = 0.571 \times \text{DTA} - 0.0056 \times \text{DTA}^2 + 0.000015 \times \text{DTA}^3 - 15.15$	0.273	79	9.90	< 0.001
40	$\zeta Gi^* = 0.511 \times \text{DTA} - 0.0048 \times \text{DTA}^2 + 0.000012 \times \text{DTA}^3 - 14.34$	0.475	79	23.80	< 0.001
50	$\zeta Gi^* = 0.175 \times \text{DTA} - 0.0018 \times \text{DTA}^2 + 0.000004 \times \text{DTA}^3 - 3.70$	0.474	79	23.80	< 0.001

Table 2. Birth date, mass and mass change data for mothers and pups on North Rona according to pupping location

(The location relatedness is categorized as either high ζGi^* , i.e. locations with higher than average (> 1 s.d. of the ζGi^* distribution at the 30 m scale) relatedness to the colony as a whole or other, i.e. all other locations where seals were sampled. Comparisons among groups use two-tailed t -tests. Dates use a value of 1 for 1st September, i.e. 36 = 6 October.)

variable	location relatedness category	n	mean	s.d.	s.e. mean	t	d.f.	significance (two-tailed)
birth date (1 = 1 September)	high ζGi^*	8	36.100	6.500	2.300	-0.952	35	0.348
	other	29	38.700	6.700	1.240	—	—	—
maternal post partum mass (kg)	high ζGi^*	8	198.000	16.300	5.760	0.193	29	0.848
	other	23	196.700	17.000	3.540	—	—	—
maternal mass loss rate (kg day ⁻¹)	high ζGi^*	7	4.450	0.480	0.180	2.130	28	0.042
	other	23	3.850	0.690	0.140	—	—	—
pup growth rate (kg day ⁻¹)	high ζGi^*	7	2.280	0.430	0.164	1.905	28	0.067
	other	23	1.950	0.390	0.080	—	—	—
mass transfer efficiency (pup growth rate/ maternal mass loss rate)	high ζGi^*	7	0.509	0.050	0.019	0.142	28	0.888
	other	23	0.506	0.038	0.008	—	—	—

colony as a whole were most clustered when the radii of inclusion were 30 or 40 m.

(b) *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 (ζGi^*). Regression models of ζGi^* values and the habitat descriptors for these locations indicated distance to access as being an important explanatory variable (table 1). These relationships were best described by a cubic model for the spatial scales of 30, 40 and 50 m (table 1) and suggested that ζGi^* 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 is the access point where it meets the sea and 300 is the maximum access value obtained inland). Elevation was also a significant explanatory variable at each scale considered, but was highly correlated (Spearman's $\rho = 0.96$, $n = 86$ and $p < 0.001$) with distance to access at these locations and, in this context at least, had less obvious biological meaning than

distance to sea. Slope featured as a barely significant variable at the 50 m 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 for this colony.

(d) *Reproductive performance and patterns of relatedness*

There were differences in individual reproductive performance data from known seals according to their ζGi^* (30 m) category. Although maternal post-partum 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). The growth rates of pups tended in a similar direction. There was no difference in the growth rate of pups according to their sex (males 2.04 ± 0.50 and females 1.88 ± 0.40) ($t = 1.005$, d.f. = 37 and $p > 0.3$). The efficiency of mass transfer for mothers (estimated by pup daily growth rate/mothers

Table 3. General linear model of pup growth rate (kg day^{-1}) according to maternal mass loss rate (MMLR) (kg day^{-1}), $\mathcal{Z}Gi^*$ location category and mother's identity for grey seals at North Rona in 1996 and 1997

(The location relatedness is categorized as either high $\mathcal{Z}Gi^*$, i.e. locations with higher than average (> 1 s.d. of the $\mathcal{Z}Gi^*$ distribution at the 30 m scale) relatedness to the colony as a whole or other, i.e. all other locations where seals were sampled. Adjusted $r^2 = 0.958$. Birth date ($F = 0.041$ and $p > 0.8$) and the interaction term between mother's identity and $\mathcal{Z}Gi^*$ location category ($F = 1.35$ and $p > 0.35$) were dropped from the model.)

source	sums of squares	d.f.	mean square	<i>F</i>	significance
model	4.91900	22	0.22400	31.265	< 0.001
intercept	0.04200	1	0.04200	5.878	0.046
MMLR	0.62300	1	0.62300	87.050	< 0.001
$\mathcal{Z}Gi^*$ location category	0.04900	1	0.04900	6.870	0.034
mother's identity	0.66100	20	0.03300	4.622	0.023
error	0.05006	7	0.00715	—	—
total	128.45600	30	—	—	—
corrected total	4.96900	29	—	—	—

daily mass loss) was the same in the two area categories. The 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 the growth rates of pups between area categories remained when only the few 1996 data were examined (2.59 ± 0.30 and 2.04 ± 0.36) ($t = 2.48$, d.f. = 15 and $p = 0.026$). There was no relationship between the ages of weighed mothers and relatedness at their location, but the small sample of ages ($n = 18$) 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 30–40 m 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, and (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, which was uncovered using this micro-satellite 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 (figure 1). However, females occupying central breeding locations contributed more to the colony than females elsewhere, probably through habitat-related fitness benefits. Females in central areas showed better intraseasonal reproductive performance in producing bigger, faster-growing pups that are likely to have higher than average survival (Hall *et al.* 2001). This self-reinforcing feedback allows certain genetic strains to become prevalent in the colony, as revealed by our snapshot of the genetic make-up of the colony (figure 2).

Locations containing seals with higher than average relatedness to the colony as a whole occurred in core areas of the North Rona colony. These locations occurred close to access points, but avoided 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.* 2001). Other proximate benefits for individuals occupying these prime locations included access to predictable resources. Breeding females require relatively flat terrain with ready access to water (Twiss *et al.* 2000b, 2001). There is an excess of suitably flat terrain on North Rona (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 the growth rates of their pups and maternal rates of mass loss according to relatedness area category could not be simply attributed to either maternal size or to North 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 probably 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 have contributed 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 the pups they produce (Pomeroy *et al.* 1999). Our analyses indicated the locations where the more successful mothers breed. Furthermore, these locations cluster in areas that 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 that, 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 that are occupied first during each breeding season are likely to be the areas that were the first to be colonized historically (Anderson *et al.* 1975; Pomeroy *et al.* 1994, 2000b; Twiss *et al.* 2000b). Here, we have demonstrated, for the first time to the authors' knowledge, 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 North Rona colony should persist.

While this approach has demonstrated a non-random distribution of relatedness among breeding female grey seals on North Rona within a season, the inter-annual stability of this pattern is unknown. The colony social structure elsewhere may be different and it remains to be seen whether a 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-scale spatial 'genetic map' of a breeding colony provides a clearer view of the factors that may influence short-term individual choices and their ultimate fitness consequences. Grey seal breeding colonies represent temporary aggregations, yet social structure is apparent. Social structure is likely to be widespread even amongst temporary or at least semi-permanent aggregations. 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.

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