Fine scale topographic correlates of behavioural investment in offspring by female grey seals (<u>Halichoerus grypus</u>).

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ABSTRACT

Grey seals breed colonially on substrates ranging from ice to rocky or sandy beaches. Clear differences in seal behaviour patterns exist among such broad classes of breeding habitat. However, finer scale topographic variation is likely to influence individual behaviour with consequences for pupping success. We examine topographic influences on breeding female grey seal behaviour by quantifying topography at a sub-seal size resolution. Using sub-metre resolution Digital Terrain Models of two sites within a rocky breeding colony we compare site topography in relation to observed differences in female behaviour at these sites. Females at both sites showed a preference for breeding close to water (standing pools or sea) and frequently commuted between their pups and water. Topographic models indicated that one site was more costly for seals in terms of their locations and movements within the site. This was due to a lack of low elevation land adjacent to the main access points from the sea and the reduced availability of pools. Females at this site showed reduced pup attendance and an increase in energetically costly behaviours, whilst females at the lower cost site spent more time interacting with their pups and resting. These topographically induced behavioural differences are likely to affect the quantity and quality of pup provisioning by mothers and influence individual pupping site selection. Less costly sites are likely to be colonised preferentially and by larger, older and more dominant females, potentially generating fine scale spatial heterogeneity in female quality within the breeding colony.

Whilst it may be obvious that topography is likely to impact significantly on an individual animal's behaviour (Stamps 1995) most studies of behaviour and habitat use that have

incorporated topographic elements have relied purely on qualitative descriptions (e.g. Anderson & Harwood 1985; Campagna & Le Boeuf 1988; Reid & Weatherhead 1988). In addition, when examining individual behaviour in relation to their physical surroundings it is important that topography is quantified at a spatial grain relevant to the behaviours being studied, that is, at a resolution whereby topographic features will actually impact upon individuals' decision making processes (Forman & Gordon 1986; Turner et al. 1989; Wiens 1989). Very few studies have achieved both these aims (e.g. Kodric-Brown 1983; Harris et al. 1997). Such studies require detailed mapping data, traditionally acquired with complex surveying techniques. However, recent advances in the application of remotely sensed data and spatial analytical tools, such as Geographical Information Systems (GIS), have provided access to such detailed information for behavioural ecologists. Digital terrain models can now be generated from easily acquired digital data for most areas of the world, at least at course spatial grains. These data may be useful for the examination of larger scale phenomena, such as animals with large home ranges, in relation to terrain (e.g. Powell & Mitchell 1998; Thomas 1993). However, the scale of topographic measurement must be close to the individual's perceptual scale (extent and resolution) in order to determine potential influences upon minute by minute behavioural decisions of individuals (Kolasa & Rollo 1991). This study achieves this resolution of topographic measurement and relates topography to individual behaviour in breeding female grey seals.

Grey seals breed on a wide variety of substrates (Stirling 1975), ranging from ice (e.g. Haller et al. 1996), through sandy beaches (e.g. Anderson & Harwood 1985; Boness & James 1979) to rugged, rocky islands (e.g. Anderson et al. 1975). Stirling (1975) stated that the grey seal "offers the greatest opportunity for study of the effects of different breeding habitats on social behaviour", yet few quantitative studies of breeding site topography have been undertaken. Early studies of grey seal breeding colonies presented purely qualitative descriptions, but suggested topographic influences on seal dispersion patterns (Boyd et al.

1962) and male and female behaviour (Hewer 1960; Hewer & Backhouse 1960; Anderson et al. 1975; Anderson & Harwood 1985). Recent quantitative analyses have provided evidence that breeding females aggregate around access gullies (Pomeroy et al. 1994). Twiss & Thomas (in press) confirmed the importance of local scale topography in determining dispersion patterns at three topographically contrasting colonies. However, dispersion patterns are determined by individual behavioural choices, and topography at a fine scale may influence the daily behaviour and energetic expenditure of individual seals during their annual breeding effort. We use high resolution Digital Terrain Models (DTMs) within a GIS to compare quantitatively two discrete study sites within the same breeding colony. We assess the physical characteristics of these sites at a spatial grain (sub-'seal size') at which topography is likely to influence individual behaviour.

On arrival at the colony, pregnant females spend up to two days selecting suitable pupping sites (Pomeroy et al. 1994; in press). Females generally remain with their pups throughout lactation, but many observers have noted the tendency for lactating females to bathe in pools of water (Anderson et al. 1975; Boyd et al. 1962; Hewer & Backhouse 1960; Pomeroy et al. 1994; Caudron 1998). When the locations of water and suitable pupping/nursing sites are spatially separated there will be increased travelling costs, in terms of time and energy expenditure, incurred by the mother. Travelling costs will depend on both the surface distance and the nature of the terrain traversed between pup and water. We use our DTMs to model the relative travel costs incurred by females in commuting between pupping/nursing sites and water bodies at our two study sites. Where access to water is more costly (or restricted) we hypothesise that females will spend more time travelling and away from their pups. Conversely, where access to water is relatively easy, we expect less movement and greater mother-pup attendance. We use detailed behavioural studies of known females and their pups at these two sites to test these hypotheses. We believe this is the first quantification of individual breeding

behaviour in relation to terrain which uses an accurate, individual perceptual scale topographic model to predict the behaviour patterns of individual animals according to the physical characteristics at and around their selected birthing location.

METHODS

Study Sites

The Isle of May lies in the mouth of the Firth of Forth, Scotland (56° 11'N, 2° 33' W). This island forms the major single grey seal breeding colony on the UK's east coast, with a total of 1408 pups born in 1994, rising to 1582 in 1996, the period covered by this study (SMRU, unpublished data). We selected two spatially discrete breeding areas within the Isle of May colony as our study sites. The northernmost site, West Rona Beach (WRB), covers 14889 m^2 (1.49 ha), the southernmost site, Tarbet, covers 14335 m^2 (1.43 ha). These sites lie within 85m to 160m of each other, but each has its own access points with little overland interchange of seals between them. Each of these sites contain approximately 25% of the pups present on the entire island at the height of the breeding season. The selection of study sites was not made with reference to topographical differences. The breeding season at the Isle of May extends from mid October to the end of November. During this period pregnant females arrive at the colony, select a pupping site and give birth to a single pup which they suckle for approximately 18 days, after which the pup is abruptly weaned. The female enters oestrus and mates immediately before weaning the pup, after which she departs the breeding site. Thus, each breeding female is present on the colony for approximately 18 to 20 days, whilst the entire breeding season spans approximately seven weeks. There is therefore a turnover of females during the season.

GIS Database and DTM Generation

We established a GIS database (ARC-INFO Version 7.0.3: Environmental Systems Research Institute Inc. (ESRI), 380 New York Street, Redlands, California, USA) from high resolution colour aerial photographs (5" x 4" format, taken at an altitude of approximately 366m) taken by SMRU for the annual grey seal census (Hiby et al. 1988). We used photographs from surveys conducted during the 1994 breeding season on the following dates; 17/10, 28/10, 14/11 and 25/11. For each date a series of three or four images provided complete coverage of our study sites. These photographs were scanned onto Kodak Photo-CD at a resolution of 4096 x 6144 pixels and then transferred to the GIS as TIFF images. We registered and rectified these images to real world co-ordinates using ground control points (GCPs) identifiable in the images and located in the field by a sub-meter accurate Carrier Phase Differential Global Positioning System. All GCPs were collected post breeding season. Once rectified, image resolution was such that one pixel was equivalent to 0.056m on the ground.

We generated DTMs of the two study sites from the images as described in Mills et al. (1997). DTMs were accurate within a 'sub-seal' size resolution, with R.M.S. (root mean square error) values ranging between 0.22 to 0.57m (Mills et al. 1997). DTMs were stored in the GIS as grid coverages representing elevation values in metres above mean sea level, with a grid cell resolution of 0.2m x 0.2m.

The positions of all breeding females and white coat pups were digitised from the rectified images, using the tip of the animal's nose as the standard reference point. Breeding females and pups were readily distinguished from adult males and weaned pups using differences in size and coloration. The digitised positions provided point coverages (topologically linked geographic features with their associated descriptive data) of seal

locations for the four dates during the 1994 breeding season. We also digitised polygon coverages of land extent and all pools of water (land locked water bodies) from the images for the same dates. Land and pool coverages were then converted into grid coverages of the same resolution and extent as the DTM grids. At the 0.2m resolution no cells contained more than one seal location.

Topographic Parameters and Cost-surface Modelling

In addition to elevation values, we used the DTMs to generate the following topographical parameters within the GIS, each represented as grids of the same extent with a cell size of 0.2m x 0.2m:

(1) Slope: the maximum rate of change in elevation from each cell to its eight nearest neighbours (measured in degrees).

(2) Aspect: the direction of the maximum rate of change in z value for each cell (measured in compass degrees).

(3) "Cost-distance" to "nearest" pool of water.

(4) "Cost-distance" to "nearest" access point (entry point to/from the sea).

Parameters 3 and 4 were generated with the cell-based cost-surface modelling procedures of the GIS. These models allowed us to investigate the potential relative costs incurred by individual animals when moving within the study sites. "Cost-surfaces" provide a cell by cell index of the cumulative cost incurred from travelling from any point on the land surface to (i) the "nearest" pool of water and (ii) the "nearest" access point. In this context "nearest" was defined as the water body yielding the least cost route, where the route from any location to pool or access point was determined by the topography of the DTM and was not necessarily a linear route and cost is a function of the slope traversed in moving from one grid cell to the next. Our aim was to produce a reasonable model of potential seal movement,

whereby slight advantage was gained by travelling down shallow to moderate gradients and increasing cost was incurred in moving up steeper slopes. In addition, near vertical cliffs of 2m height should present an unassailable barrier to movement requiring individuals to deviate around such obstacles (grey seals are approximately 2m in length and can, with some difficulty, climb near vertical faces slightly shorter than their body length (AC, PPP, SDT, pers. obs.)). Thus, modifiers were incorporated into the models which determined the relative cost (vertical factor, VF) incurred in moving from one cell in the grid to an adjacent cell dependent upon the elevation change. VF was calculated as the cosine function of all negative slopes encountered (downhill movements) and the secant function of all positive slopes (uphill movements). Both cosine and secant functions were raised to the power of 2 to provide the final VF values. Where positive or negative angles were in excess of 84° the VF was set to infinity. Thus, elevation changes between successive cells of 2m or more form an impenetrable barrier to movement. These models assume that the route taken is always via the least cost adjacent cell, and the ultimate value assigned to each cell is the accumulation of all VFs encountered on the route from that cell to the access point or pool. Our cost-surface models therefore provide a relative index of the proximity to pools and access points for each cell in the DTMs, whilst accounting for topographic features. Note that our use of the term 'cost' with respect to these models implies no direct assessment of any physiological cost to individual seals, merely a relative index of the distance and potential ease or difficulty in accessing pools or the sea from any point in our study sites. We generated cost-surfaces only once for access points, however, separate cost-surfaces were generated for each date for pools. This is because the number, extent and distribution of pools of water alters during the breeding season.

We produced frequency histograms of cell values for all the above topographical parameters for each site, firstly depicting values for all grid cells in each DTM and secondly, for only those grid cells which contained breeding females on land. The former represented a

description of the 'available' topography, whilst the latter was effectively a description of topographies that were 'utilised' by breeding females whilst on land. We used Kolmogorov-Smirnov two sample tests to conduct inter-site comparisons for each parameter.

Female and Pup Dispersion Patterns

For each date we used the spatial tools of the GIS to compute distances (in metres) from each white coat pup to the nearest breeding female within the respective point coverages. Data were downloaded into SPSS (Version 5) in which we compared natural log-transformed distances by date and site by ANOVA with Scheffe's multiple range test at a significance level of 0.05. Individuals cannot be identified solely from the GIS database, thus these measurements were from each pup to the nearest female, irrespective of whether that female was the pup's mother or not. We computed distances (in metres) from each female to her nearest female neighbour for each date from the respective point coverages within the GIS. Data were downloaded into SPSS where comparisons of natural log transformed distances by date and site were made by ANOVA with Scheffe's multiple range test at a significance level of 0.05. Female coverages were used to determine the maximum densities of females observed in each occupied 10m x 10m grid cell within each site. This grid cell size yields maximal measures of aggregation of females (S.D. Twiss, unpublished data, see also Pomeroy et al. 1994, Pomeroy et al. in press) whilst providing a reasonable range of density values for comparative purposes. Furthermore, this quadrat size was below size of the defined areas of suitable pupping terrain for grey seals at these sites (Pomeroy et al. in press, Twiss & Thomas in press). The resulting distributions of maximum densities for each site were compared using Mann-Whitney U tests.

Measuring Female Sizes and Estimating Mass from Aerial Photographs

We used the GIS to measure the length and width of breeding females from the images of the two sites and adjusted these measures for proximity to the camera by using the elevation value for each seal's location as derived from the DTMs as described in detail in Twiss et al. (in press). We measured only those seals that were lying straight on relatively flat terrain and where the nose and posterior end of body were clearly visible. These measurements were then used to estimate each individual's mass (Twiss et al. in press, equation provided in Table 8). We separated data from the four dates into early and late season periods based on the timing of peak oestrus, the date on which the maximal number of females were likely to be in oestrus. Peak oestrus date was defined as peak pupping date + 18 days (the average time from parturition to entering oestrus). Peak oestrus date at WRB and Tarbet in 1994 was on the 6th of November. We used t-tests to compare between sites for both early and late periods. All data sets conformed to normal distributions with the exception of estimated mass for Tarbet during the early season period, therefore estimated masses for the early season comparison were log transformed.

Behavioural Observations

We recorded behavioural observations from hides overlooking the study sites. Observations of mother pup pairs at both sites were carried out between 23/10 and 28/11 during the 1994, 1995 and 1996 breeding seasons. Study females were individually identified using pelage patterns, temporary dye marks, or permanent brands. During half hour scanning sessions, we recorded the behaviour of mothers and pups of between five and 12 pairs every two minutes along with mother-pup distances (estimated in adult body lengths and daily means and maximums calculated). Also, the substrate type on which the mother and pup were situated was recorded at the same intervals. We classified substrate as either mud, rocks, tidal access pools (equivalent to the access points in the GIS database) or as puddles (rain or sea spray filled

land locked pools equivalent to the pools in the GIS database). Scan sessions between 09:30 and 17:00 GMT were alternated with non-scanning half hours when complementary information was collected. Approximately 50% of observation days were devoted to each study site (50 days at WRB, 52 days at Tarbet) and observers were alternated between sites each day.

We described the behaviour of mothers by six mutually exclusive categories: (1) resting (sleeping and low energy cost non-social behaviours such as comfort moves), (2) alert (head up, neck stretched and looking around), (3) non-sexual aggressive interactions, (4) interactions with their pup (feeding, flippering, nosing or playing with pup), (5) locomotion (movement resulting in a change of location) or (6) sexual interactions (attempted and successful copulations). We described pup behaviour by three mutually exclusive categories: (1) resting, (2) active, or (3) suckling (pup's mouth in contact with mother's nipple). Activity budgets were estimated by the percentage of scans corresponding to each category (Altmann 1974; Martin & Bateson 1993).

We treated these data as five different sub-sets, with the individual-day as the statistical unit: female behaviour and the substrate type for females (n = 778 female-days with 145 different individuals), pup behaviour and the substrate type for pups (n = 546 pup-days with 92 different individuals) and mother-pup distances (n = 586 pair-days with 99 different mother pup pairs). Relations between the response (behaviour, substrate type, mean or maximum mother-pup distance) and ten potential explanatory variables were analysed with Generalised Linear Models using GLIM 4.0 (Francis et al. 1993; Lindsey 1995). These ten variables were:

(1) year,

(2) date during the breeding season,

(3) female age class: (i) less than 19 years old, (ii) greater than or equal to 19 years old (a cut off at 19 years effectively divided the known age females into study females from recent (i) and previous (ii) marking efforts) and (iii) of unknown age,

(4) stage of the breeding season at which the mother gave birth, classified as (i) before 25% of births, (ii) between 25% and 75% of births, or (iii) after 75% of births in the study areas (this classification was based upon the relative ages, sizes and success of individuals at the various stages of the season (see Pomeroy et al. 1999)),

(5): pup's location with respect to proximity to water bodies and maternal movements: each female-day was classified into five exclusive categories based on the distance from the pup's location to the nearest water bodies and on the 'commuting' behaviour of the mother on the day in question. These categories are intended to express the hypothesis that greater distances travelled increases potential costs to the female, not only in terms of distance, but also in terms of the likelihood of increased aggressive interactions on the way to the pool (a function of distance) and the number of individuals encountered and therefore interactions whilst in the pools (a function of pool size and usage). These categories are as follows and increase in potential cost i.e: (i): the pup was > 25m from any tidal pool and the mother did not bathe for the whole day, (ii): the pup was > 25m from any tidal pool but close to a puddle that the mother visited at least once on that day, (iii): the pup was close to (within tidal range) a tidal pool that the mother visited at least once on that day, (iv): the pup was moderately close to (above the highest tide level) an access pool that the mother visited at least once on that day, (v): the pup was distant (> 25m) from any tidal pool that the mother visited at least once on that day.

(6) pup age (younger than 3 days, between 3 and 14 days, older than 15 days (i.e. from the beginning of moulting)),

(7) presence or absence of a brand on the mother (branded females have been the subject of long term monitoring programmes requiring repeated capture, thus inclusion of this variable account for any potential effects upon these individuals),

(8) minor disturbance at the periphery of observation area (yes or no). Causes of disturbance included movements of people along a pathway adjacent to the Tarbet site and the presence of boats close to the shores of the two sites.

(9) observer identity (three different observers, with AC making observations all three years),

(10) study site (WRB or Tarbet).

The model used allowed the effect of study site to be investigated when the effects of the nine other variables were controlled. We compared the behaviour of mothers and pups and the substrate type on which they were situated (the response variables) between WRB and Tarbet in models incorporating the effects of all ten variables described above. These models provided equations giving the expected values of the response variables calculated from the combined interactions of the ten putative explanatory variables. We then examined the proportion of the observed variability in the response variables that was explained by study site (variable 10) whilst controlling for the remaining nine variables. As data for maximum and mean daily mother-pup distances were qualitative, models describing these responses incorporated only those variables giving the lowest Akaike Information Criterion (AIC) (Lindsey 1995).

The models were fitted with GLIM using the Poisson representation of the multinomial distribution. This involves the canonical log link. This takes into account dependence among the behavioural categories as the sum of probabilities for all categories is one. Residuals for the final models were visually inspected and showed no unexpected anomalies.

RESULTS

Inter-site Topographical Comparisons

Available topography (all grid cells)

We found significant differences between sites in all topographical measures (Table 1). The largest difference was in the distribution of elevation values. WRB had a large proportion

(39.3%) of land at low elevation (between 0 and 4m above mean sea level). Tarbet was essentially lacking in land of this low elevation (Figs. 1a and b), having only 4.5% of its area at elevations below 4m. This was reflected in the distributions of "cost-distance" to access points. WRB possessed a high proportion of land with low "cost-distance" to access. In contrast, Tarbet had very little area of low "cost-distance" to access, with its higher elevation areas requiring long or steep slopes from the access points. These data suggest that movement to and from access points was generally more difficult at Tarbet. Comparisons between the two sites for "cost-distance" to "nearest" pool showed the most extreme differences at the start of the breeding season (17/10/94), with WRB tending to have relatively more low cost area than Tarbet. These differences then diminished through the season (Table 1), until on the final date (25/11/94), the pattern was reversed and Tarbet had slightly more low cost area than WRB. Again, these data suggest that movement to and from pools of water was generally more difficult at Tarbet.

Areas utilised by breeding females (grid cells containing seals)

Seals at Tarbet occupied sites with greater "cost-distance" to an access point and at higher elevations than those at WRB (Figs. 2a to f, Table 2). Similarly, seals at Tarbet were located at sites with greater "cost-distance" to pools of water than seals at WRB, during the early (28/10/94) and mid (14/11/94) part of the season, although there was no significant difference towards the end of the season (25/11/94). As both surface distance and topographic complexity contributed to our "cost-distance" indices these results suggest that seals at Tarbet were generally found further, in terms of accessibility, from access points and pools of water than seals at WRB. There were no differences between sites in either slope or aspect values of sites occupied by seals.

<u>Number and size of pools of water during the breeding season</u>

At both sites the total and median area of pools increased through the breeding season (Table 3). There was no significant differences between sites in the median pools sizes throughout the breeding season, the Tarbet study site was characterised by having a larger number of pools, which together provided a greater area of water than at WRB. Larger pools at these sites also tend also to be deeper ones (per obs. SDT, PPP).

Differences Between Sites in Breeding Female Behaviour

Study site had a significant effect on female behaviour and substrate type for both mothers and pups (deviances in GLIM models significantly decreased compared to a saturated multinomial model - see Tables 4 and 5). Thus, the relative contribution of study site to explaining the variability in these three response variables was significant, even in models containing all nine other putative explanatory variables. We found no significant differences in pup behaviour between the two sites. Mothers at WRB spent more time in resting, non-sexual aggressive interactions, interacting with their pups and slightly more time alert than mothers at Tarbet which were more mobile and spent more time in sexual interactions. Using combined data from both study sites it was evident that mothers spent a considerable time in water (mean = 27.6 % ± 1.15% of observation time, n = 778 female-days), whilst pups were rarely found in water (mean = 4.0 % ± 0.17% of observation time, n = 546 pup-days). Comparing between sites, both WRB mothers and their pups spent more time in muddy and rocky areas than their Tarbet counterparts, which were found more often in pools or puddles.

Both daily mean and maximum distances between mothers and pups (estimated in adult body lengths) were greater at Tarbet than at WRB, when the effects of other variables were controlled (Table 6). For mother-pup distances, the models providing the lowest AIC values

included the effects of study site, the pup's location with respect to proximity to water bodies and maternal movements, year and observer identity. Inclusion of observer in this model indicated observer differences in the estimation of mother-pup distances as adult body lengths. However, analyses of actual pup to female distances measured within the GIS showed differences between WRB and Tarbet (Fig. 3) agreeing with those shown through the behavioural observations. On 14/11/94, pup to nearest female distances (natural log transformed) were significantly greater at Tarbet than at WRB (ANOVA: $F_{7,1792} = 67.0$, p < 0.0001). The remaining three dates showed no significant differences, although Tarbet had greater mean distances than WRB for two of these dates. When all four dates were combined, there was a significant difference between sites (WRB; n = 1069, mean = 1.11 ± 1.0, Tarbet; n = 731, mean = 1.38 ± 1.0, t-test; t = -4.93, p < 0.001).

Female Dispersion Patterns

Both sites showed seasonal variation in inter-female nearest neighbour distances (natural log transformed) with maximal aggregation on 28/10/94 (Fig. 4). However, throughout the entire season females at WRB showed a greater degree of aggregation than those at Tarbet, with nearest neighbour distances at WRB being significantly smaller than those observed at Tarbet (ANOVA: $F_{7, 1345} = 26.04$, p < 0.0001). This was confirmed by our comparison of maximum female densities observed in 10m x 10m grid cells with WRB showing a significantly greater median density than that observed at Tarbet (Mann-Whitney U = 3258, n1 = 78, n2 = 103, z = -2.29, p = 0.022).

Female Size and Estimated Mass

During the early season period there were no significant differences (at $p < 0.05$) between sites in the widths, estimated masses or mass:length ratios of females (Table 7). However, females at WRB were significantly longer than those at Tarbet. There was an indication that heavier females were present at WRB ($p < 0.1$) although this was not significant at $p < 0.05$. We detected no differences in the late season period (Table 7).

DISCUSSION

Here we have applied new techniques to identify fine spatial grain topographic characteristics of seal breeding sites and have used topographic models to predict behavioural consequences of topographical variation for breeding seals. Within a small island such as the Isle of May it is inevitable that broad qualitative topographical classifications will do little to elucidate topographical differences between sub-sites. Through our use of accurate DTMs we have achieved a measurement resolution sufficiently fine to distinguish broadly similar sub-sites as topographically and functionally different. This spatial grain was also appropriate for assessing topography at a resolution that individual seals use when making decisions (Forman & Gordon 1986, Kolasa & Rollo 1991, Turner *et al*. 1989, Wiens 1989). Our topographic analyses suggested that the Tarbet site was a relatively higher "cost" site than that of WRB. Access to both sites was restricted to tidal inlets running up gullies from the sea. The main difference between sites lay in the lack of low lying land at Tarbet. Seals entering the Tarbet site were required to traverse a steep slope unsuitable for pupping, in order to reach ground flat enough for pupping (all females were on slopes of less than 45°). These sites were at higher elevation than those immediately available upon coming ashore at WRB. In consequence, distances from pupping sites to access points were increased at Tarbet.

Secondly, the distribution of pools of water differed at the two sites. In the UK grey seals show a preference for breeding close to water, in which mothers spend considerable time, as shown by our data (see also Anderson et al. 1975; Boyd et al. 1962; Hewer & Backhouse 1960; Pomeroy et al. 1994). In contrast, their pups spend very little time in water. Thus, whilst "bathing" at a pool, mothers will inevitably be separated from their pups to some degree. Females at WRB were able to attain pupping positions relatively close to pools compared to females pupping at Tarbet. At Tarbet fewer females gained pupping sites close to pools of water and their physical access to it was more difficult, as indicated by the greater "cost-distance" to pools at this site. Tarbet is a more broken, rocky site, with smaller areas of relatively flat, muddy substrate which form the main pupping sites. At WRB the greater proportion of suitably flat substrate around pools (low cost areas) allowed many seals to obtain pupping sites close to pools. This was supported by the measurements of breeding female dispersion patterns which indicated that females at WRB were more aggregated throughout the season than at Tarbet. Towards the end of the autumnal breeding season, increased rainfall and storm driven sea-spray leads to increased numbers of pools being available, while the number of females breeding is declining. These factors allow the remaining females to disperse more without increasing cost, thus removing any site difference in the "cost-distance" values to pools of water.

Behavioural differences observed at our study sites corresponded with our prediction that mothers at sites where movement between pups and water was more difficult, as determined by our topographic models, should spend more time away from their pups. Mothers at Tarbet spent more time in locomotion and away from their pups and less time interacting with their pups compared to mothers at WRB. These differences appear to be associated with the greater cost and distance of commuting from the mothers' locations to available access points (sea) at Tarbet, thus, restricting "bathing" opportunities to pools of water. Females at

WRB were relatively closer to both access points and pools of water (at least during the early and mid parts of the season), thus requiring less locomotion and less time away from their pups. Mothers at Tarbet also spent relatively more time in pools of water despite the greater difficulty of accessing pools from their pupping sites. In combination with the reduced pup attendance, this suggests that the greater commuting costs at Tarbet induced females to make fewer, but longer trips to water, whilst at WRB mothers could readily move between their pups and water. This was also reflected in the mother-pup distances as derived from intensive scans of relatively few mother-pup pairs and confirmed by our broader GIS analysis of pup to female distances. Although we could not state from the GIS that the nearest female to a pup was its mother, this was a very conservative measure of pup to mother distances. If a mother was attending her pup, there was a high probability that the nearest female was indeed the pup's mother, if, however, the mother had departed from the pup, it was more likely that the nearest female to the pup was not its mother. Therefore, this analysis was biased towards minimising the effect of non-attendance of mothers (at colonies including the present study sites Worthington-Wilmer et al. in press(a) have recently demonstrated via micro-satellite analyses that, based on proximity, approximately 88% of pups were the offspring of their nearest adult female). Despite this, the GIS based analyses showed significant differences in the same direction as the behavioural records and have provided more general data on a vastly increased sample. This illustrates how measures available from the GIS database can reflect individual behavioural patterns. Whilst this is a valuable application of GIS techniques to studies of animal behaviour, we were, in this study unable to identify specific individuals from the aerial photographs. Ideally unobtrusive methods would be employed by which known individuals can be located accurately within DTM's for example, and in real time in the field. Future developments of our application of GIS will aim to incorporate this feature. For our GIS based dispersion analyses we used data from 1994 only, whilst our behavioural observations were from three consecutive seasons,

however, patterns of colonisation and site use at the Isle of May are consistent between years (Pomeroy et al. in press).

Although being less active overall, WRB females spent more time in non-sexual aggressive interactions than Tarbet females. This is likely to be a consequence of the smaller nearest neighbour distances at WRB. Females in denser aggregations will experience greater rates of intra-sexual interactions. Tarbet females spent more time in sexual interactions than those at WRB. Differences in levels of sexual activity may be associated with differences in mobility. The more mobile Tarbet females are likely to encounter male attention more often and trigger more sexual investigations. This will again reduce pup attendance and increase energy expenditure. Boness et al. (1995) documented reduced maternal performance as a result of increased male harassment in grey seals.

With the exception of intra-sexual aggression, mothers at Tarbet spent more time in energetically expensive behaviours and less time with their pups than mothers at WRB. These behavioural differences were clearly influenced by topography, in particular access to water. Levels of mother-pup attendance and expenditure of energy in active behaviours will influence the rate of provisioning of the pup if the period of separation conflicts with the frequency of suckling. Pup mass gain during lactation may then vary with colony topography, and may ultimately affect longer term survival of weaned pups as they leave the island, relying on their blubber reserves whilst learning to forage. Irrespective of such energetic considerations, separation of pups from their mother has been shown to increase pup injuries and mortality in a variety of pinnipeds; southern (Mirounga leonina) and northern (M. angustirostris) elephant seals (see Baldi et al. 1996), South American fur seals (Arctocephalus australis) (Harcourt 1992), Antarctic fur seals (A. gazella) (Doidge et al. 1984) and in grey seals (Anderson et al. 1979; Baker & Baker 1988; Pomeroy et al. 1994).

Early season females at Tarbet were shorter than those at WRB. Longer females tend to be older, more experienced breeders and heavier females produce pups of greater mass at birth and at weaning although this relationship is complicated by interactions with body length (see Pomeroy et al. 1999). Pomeroy et al. (1999) suggest that reproductive senescence or greater metabolic overheads may account for the reduction in performance of the longest females in a long term study of known individuals at North Rona (Scotland). However, they do show that the smallest, youngest females had the lowest pupping success rates. Smaller females (in terms of length and relative mass) breed later in the season (Fedak & Anderson 1982, Pomeroy et al. 1999, Twiss et al. in press). Here, our data suggest an additional spatial difference, at least during the early season period, with many smaller females selecting (or being forced to select) less topographically suitable sites. Older, longer females may also be more socially dominant and with a tendency to pup earlier in the season are likely to have first choice of available pupping sites (Pomeroy et al. 1999, Pomeroy et al. in press, Twiss et al. in press). Later arriving individuals will have a reduced selection of sites. The greater aggregation and densities of females at this site correspond with the more favourable topographic and behavioural measures suggesting that WRB was the preferred site. However, no site differences nor density dependent effects upon pre-weaning pup-mortality or morbidity were discerned at these sites (Pomeroy et al. in press) although our data show site differences in behavioural costs related to local topography. Intra-colony differences in fine spatial grain topography may form an important component in individual pupping site choice and the colonisation sequence within seasons (Pomeroy et al. in press). These choices will determine the location and composition of female aggregations within the colony potentially producing heterogenous distributions of females in terms of their body sizes, ages and dominance. Such fine scale social structure would spatially stratify the quality of potential mating partners within the breeding colony (Twiss et al. 1994, Worthington-Wilmer et al. in press(b)).

ACKNOWLEDGEMENTS

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1   **Table 1.** Comparison of topographical values in all grid cells in the WRB and Tarbet DTMs (available topography) using Kolmogorov-Smirnov tests,

2   and medians, lower and upper quartiles of topographical parameters for all grid cells in the WRB and Tarbet DTMs (available topography).

3

Topographical parameter	No. of cells				WRB			Tarbet		
	WRB	Tarbet	K-S z	P	lower quartile	median	upper quartile	lower quartile	median	upper quartile
Elevation	6630	6382	20.41	< 0.001	2.56	5.23	8.71	5.98	6.86	8.26
Slope	6630	6382	3.78	< 0.001	5.99	15.76	27.30	5.90	15.65	31.85
Aspect	6630	6382	8.56	< 0.001	42.04	176.22	283.20	33.69	135.00	230.84
"Cost-distance" to access	6630	6382	15.17	< 0.001	12.75	24.25	41.84	23.50	42.26	55.37
"Cost-distance" to pool - 17/10/94	6630	6382	8.37	< 0.001	7.88	17.68	35.10	8.73	25.05	46.73
"Cost-distance" to pool - 28/10/94	6592	6384	2.88	< 0.001	7.79	15.54	31.80	7.13	17.83	32.08
"Cost-distance" to pool - 14/11/94	6658	6384	2.77	< 0.001	6.51	14.99	31.85	6.79	16.86	34.81
"Cost-distance" to pool - 25/11/94	6624	6384	4.20	< 0.001	6.22	15.55	32.79	5.32	15.08	27.38

4

1 **Table 2.** Comparison between study sites of topographical values in only those grid cells

2 containing seals (utilised topography) using Kolmogorov-Smirnov tests

3

Date	28/10/94		14/11/94		25/11/94	
No. of cells - WRB : Tarbet	62 : 53		118 : 88		41 : 18	
	K-S z	P	K-S z	P	K-S z	P
Elevation	5.25	**< 0.001**	5.63	**< 0.001**	2.75	**< 0.001**
Slope	1.39	0.041	0.66	0.778	1.28	0.078
Aspect	1.41	0.038	0.86	0.458	0.99	0.284
"Cost-distance" to access	4.68	**< 0.001**	3.38	**< 0.001**	1.95	**0.001**
"Cost-distance" to pool	2.44	**< 0.001**	2.10	**< 0.001**	0.46	0.984

4

5 Results are presented for three dates during the breeding season as sample sizes for 17/10/94

6 were too small to permit analyses. Note: In all comparisons showing significant differences

7 median, lower and upper quartile values for WRB were less than those for Tarbet.

1   **Table 3.** Number, median and total area (m^2) of pools of water present within each study site on

2   each of the four dates during the breeding season for which GIS coverages are available

3

Site		WRB			Tarbet	
Date	n	median area	Total area	n	median area	Total area
17/10/94	36	0.34	48.4	75	0.24	84.9
28/10/94	22	0.91	61.8	34	0.64	109.7
14/11/94	27	0.96	107.4	40	0.85	133.7
25/11/94	28	1.37	115.9	80	0.61	205.1

4

1   **Table 4.** Summary statistics from GLIM examining the effect of study site on mother activity

2   budgets and substrate type

		WRB (n = 391 f-d)	Tarbet (n = 387 f-d)	SLOR
Mother Behaviour	Rest	79.09 (37.93-100)	77.11 (29.21-98.91)	-0.277
Effect of Site P < 0.001	Alert	10.42 (0-40.2)	11.43 (0-40)	-0.069
Deviance = 151.5, 5 df	Agg Int	1.72 (0-22.5)	1.79 (0-15.62)	-0.254
	Int Pup	5.19 (0-31.82)	4.55 (0-35.48)	-0.144
	Loc	0 (0-16.28)	1.96 (0-16.66)	+0.380
	Sex Int	0 (0-19.15)	0 (0-29.21)	+0.364
Substrate type (mothers)	Mud	83.34 (0-100)	22.58 (0-100)	-0.296
Effect of Site P < 0.001	Rocks	0 (0-100)	6.35 (0-100)	-0.206
Deviance = 812.3, 3 df	Pool	0 (0-100)	28.32 (0-100)	+0.476
	Puddle	0 (0-97.44)	0 (0-100)	+0.026

3

4   Abbreviated behavioural categories for mothers are: Agg Int (Aggressive interaction), Int

5   Pup (Interaction with Pup) and Loc (Locomotion). Sample sizes are given as number of

6   female-days (f-d). Summary data are presented as median percentage of scans recording

7   each activity or substrate category with ranges in parentheses for both WRB and Tarbet.

8   WRB measurements were constrained to 0, with Tarbet values compared to this baseline.

9   The sign of the standard log odds ratios (SLOR) shows the direction of variation of Tarbet

10   from WRB (Lindsey 1995) such that -ve signs indicate lower percentages for Tarbet than

11   WRB, and +ve signs indicate higher percentages for Tarbet than WRB. The decrease of

12   deviance (D) is the difference between the deviance associated with the saturated

13   multinomial model and that of the simplified model with the 10 variables used. It provides

14   an assessment of the general validity of the models. The value for mother behaviour was

1   D=2858.6, df=205 and for substrate type was D=4952.9, df=126. This value follows a χ^2

2   distribution and is highly significant in both cases (p<0.001).

3

4

Table 5. Summary statistics from GLIM examining the effect of study site on pup activity

budgets and substrate type

		WRB (n = 267 p-d)	Tarbet (n = 279 p-d)	SLOR
Pup Behaviour	Rest	67.16 (6.67-100)	66.13 (5.26-92.71)	-0.041
Effect of Site 0.1 > P > 0.05	Active	29.69 (0-93.33)	30.51 (3.28-94.74)	+0.008
Deviance = 5.2, 2 df	Suckle	2.11 (0-27.08)	2.7 (0-21.82)	+0.033
Substrate type (pups)	Mud	100 (0-100)	40.74 (0-100)	-0.942
Effect of Site P < 0.001	Rocks	0 (0-100)	41.33 (0-100)	-0.124
Deviance = 1727, 3 df	Pool	0 (0-77.03)	0 (0-82.29)	+0.560
	Puddle	0 (0-37.11)	0 (0-52.68)	+0.506

3

4   Sample sizes are given as number of pup-days (p-d). Summary data are presented as

5   median percentage of scans recording each activity category with ranges in parentheses for

6   both WRB and Tarbet. WRB measurements were constrained to 0, with Tarbet values

7   compared to this baseline. The sign of the standard log odds ratios (SLOR) shows the

8   direction of variation of Tarbet from WRB (Lindsey 1995) such that -ve signs indicate

9   lower percentages for Tarbet than WRB, and +ve signs indicate higher percentages for

10 Tarbet than WRB. The decrease of deviance (D) for pup behaviour was D=538.2, df=38,

11 and for substrate type D=5750, df=48, significant at p<0.001 in both cases.

12

13

14

1   **Table 6.** Summary statistics from GLIM examining the effect of study site mother-pup

2   distances

Mother-pup distance (in adult body lengths)	WRB (n = 285 p-d)	Tarbet (n = 301 p-d)	SLOR	Model fitted
Maximum Daily Distance	2 (1-10)	6 (1-10)	+0.388	Distribution Gamma: AIC = 2663 (decreased from 2907)
Mean Daily Distance	1.24 (1-9.05)	2.27 (1-10)	+0.319	Distribution Inverse Gauss: AIC = 1625 (decreased from 1898)

3

4   Mother-pup distances were estimated in adult body lengths and are presented as median values

5   with ranges in parentheses. AIC values are presented for models explaining variability in

6   maximum and mean daily mother-pup distances, with the AIC decrease representing the effect

7   of study site in models incorporating study site, pup's location with respect to proximity to

8   water bodies and maternal movements, year and observer identity. . The best fitting

9   distributions were Gamma for the Maximum daily distance and Inverse Gauss for the Mean

10   daily distance.

1 **Table 7.** Comparison of width, length, estimated mass and mass:length ratio between sites for

2 early and late season females.

3

Variable	early/late	mean (s.e.) Tarbet	mean (s.e.) WRB	t-value	P
Width (cm)	early	47.49 (0.57)	48.57 (0.83)	-1.09	0.278
	late	43.83 (0.47)	44.56 (0.67)	-0.92	0.358
Length (cm)	early	144.61 (1.03)	150.59 (1.57)	-3.25	**0.001**
	late	138.46 (0.95)	140.31 (0.98)	-1.32	0.188
Estimated mass (kg)	early	146.03 (3.51)	157.28 (5.09)	-1.80	0.073
	late	119.30 (2.55)	124.02 (3.44)	-1.13	0.261
Mass:Length ratio	early	1.0 (0.02)	1.04 (0.03)	-1.07	0.285
	late	0.855 (0.02)	0.880 (0.02)	-0.99	0.323

4

5 Estimated mass, mean and standard errors are provided in kg, however, t-tests were conducted

6 on log transformed data for the early season comparison.   Early season sample sizes; Tarbet =

7 137, WRB = 65, d.f. = 200. Late season sample sizes; Tarbet = 140, WRB = 97. d.f. = 235.

8 Estimated mass was derived from the following equation;

9 $\log10$ (estimated mass) = -2.75 + (1.016 x $\log10$(V)) - (0.000584 x date) - (0.419 x $\log10$(r)

10 where V is the volume of the seal estimated using a crude cylindrical model ($\Pi r^2 h$, where r =

11 radius of the axilliary girth (assumed to be circular), and h = nose to tail length). Note: volume

12 is in cm^3, radius in cm and date measured in days relative to peak pupping date (see Twiss et al.

13 in press).

14

15

Figure legends

Figure 1a and b. Frequency histograms of elevation values in all grid cells within the WRB (a) and Tarbet (b) DTMs.

Figure 2a to f. Frequency histograms of elevation, "cost-distance" to "nearest" access point and "cost-distance" to "nearest" pool values in only those grid cells containing breeding females for WRB (2a, c and e) and Tarbet (2b, d and f) DTMs. Histograms are only shown for those parameters showing significant differences between sites (Table 2). Note that the data shown combine values for all four dates within each histogram.

Figure 3. Plot of seasonal changes in mean distances (natural log transformed) from pups to the nearest breeding female at the WRB and Tarbet in 1994. Crosses indicate standard errors. Note: date is expressed in days relative to the 1st of September. Sample sizes are provided as annotation.
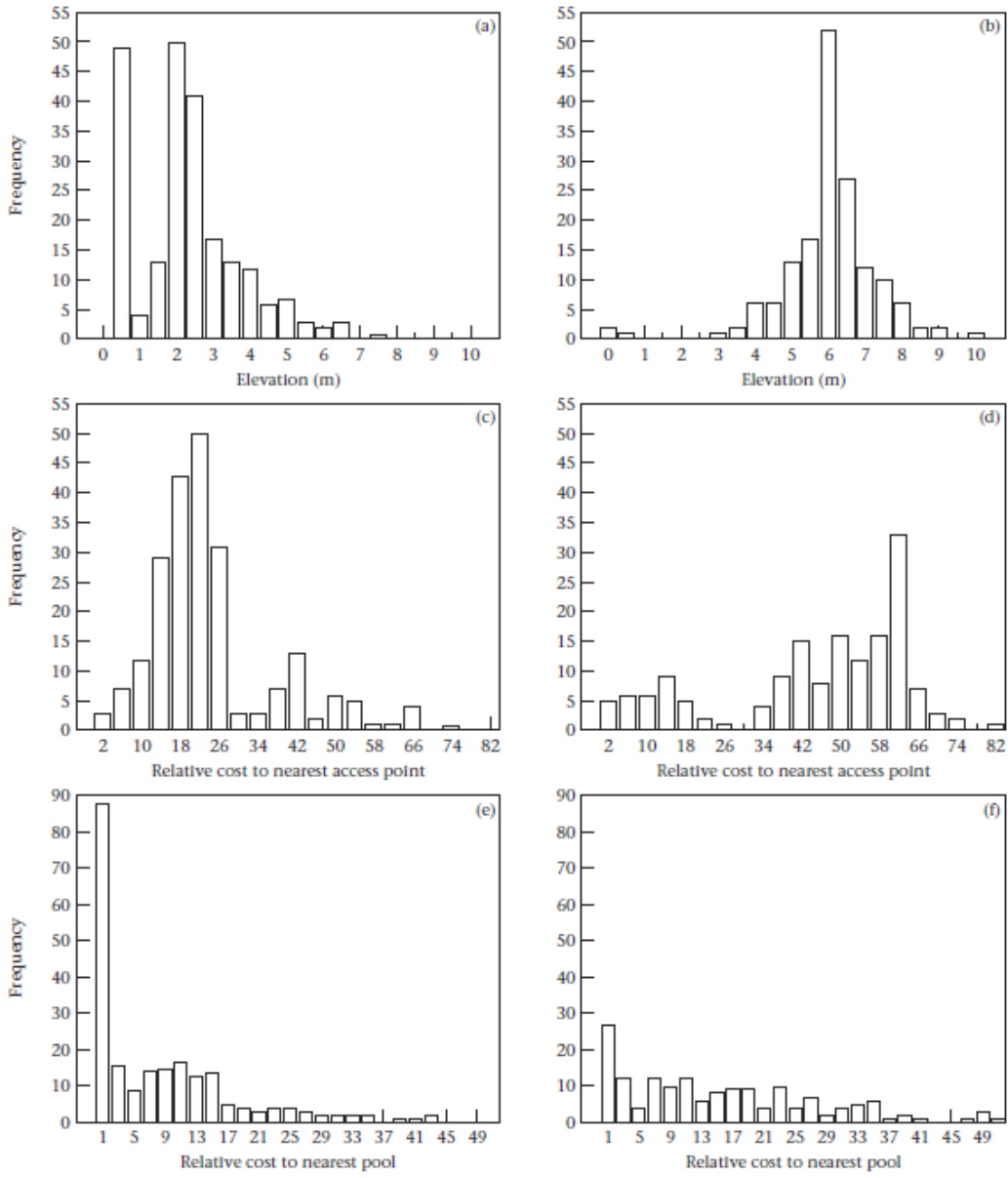
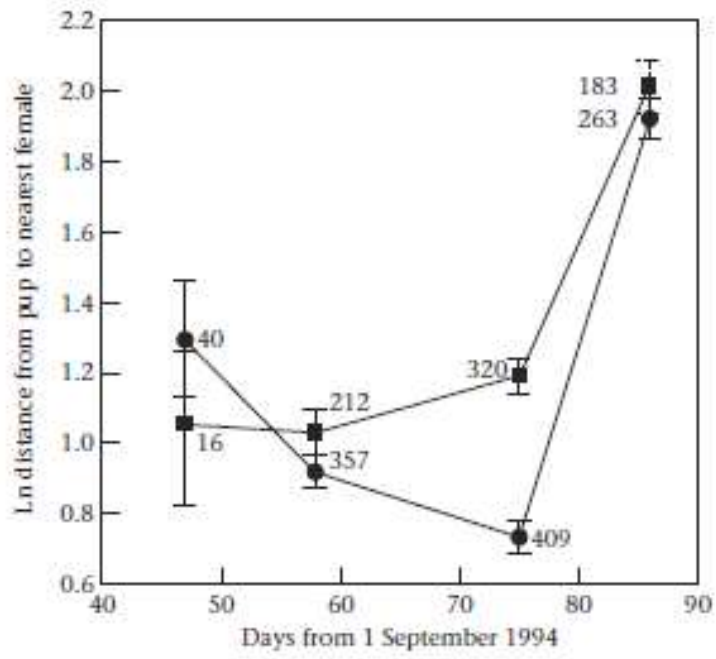**Figure 4.** Plot of seasonal changes in mean natural log transformed nearest neighbour distances for breeding females at the WRB and Tarbet in 1994. Crosses indicate standard errors. Note: date is expressed in days relative to the 1st of September. Sample sizes are provided as annotation.
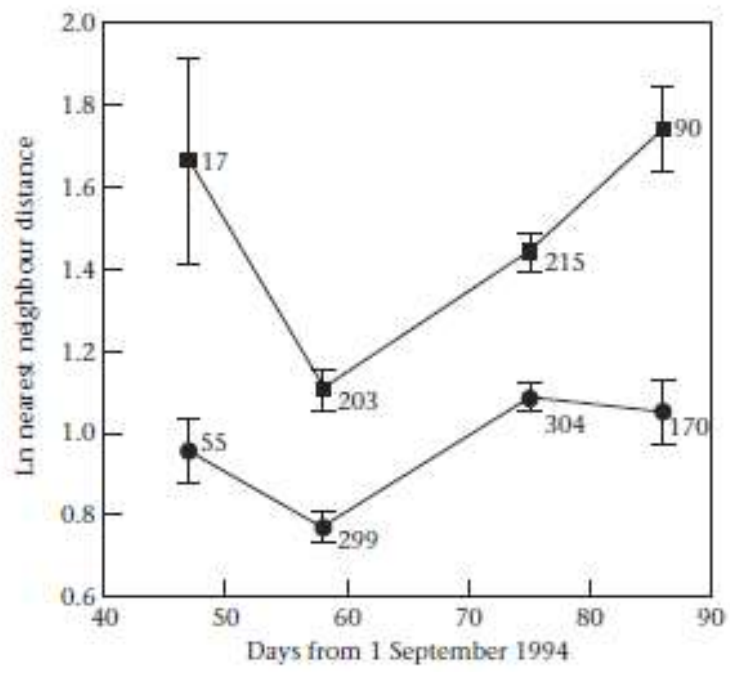
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2   Figure 1

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4   Figure 2

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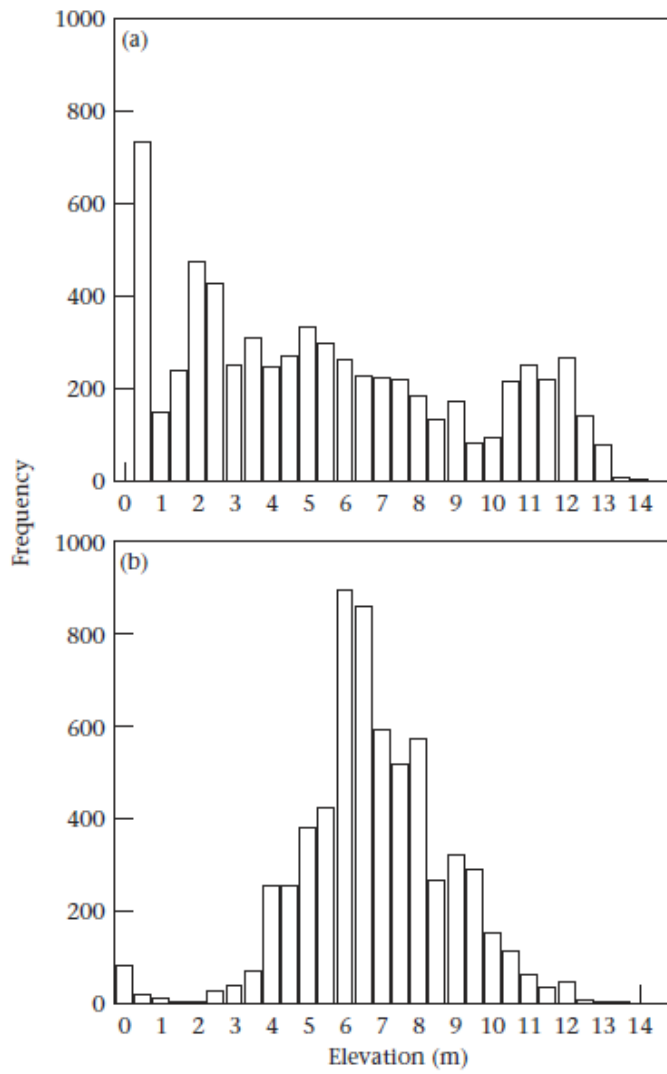
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2   Figure 3

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2   Figure 4

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