Influence of the Physical Environment and Conspecific Aggression
on the Spatial Arrangement of Breeding Grey Seals

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Abstract

Understanding the habitat requirements of a species for breeding is essential for its conservation, particularly if the availability of suitable habitat is a limiting factor for population growth. This is postulated to be the case for grey seals, one of the more abundant marine apex predators in northern European waters. In common with similar studies that have investigated the habitat preferences of breeding grey seals, we use abiotic (topographical, climatological) attributes but, unlike previous work, we also incorporate behavioural variables, particularly the occurrence of aggressive interactions between females and the presence of neighbouring seals. We used two generalized additive models (GAM) in a sequential and iterative fashion. The first model links the occurrence of aggression at particular points in the colony to local topography derived from a Geographical Information System (GIS), presence of neighbouring seal pups and the day of the breeding season. The output of this GAM is used as one of the explanatory variables in a GAM of daily variation in the spatial distribution of births. Although proximity of a birth site to a water source and the presence of neighbouring seal pups both had significant influences on the distribution of newborn pups over time and space, at the scale of the study site it was found that simple rules could predict pup distribution more efficiently than a complex individual-based simulation model.

Key-words: Generalized Additive Models; GIS, habitat suitability; individual-based model; pupping site selection; spatial and temporal simulation modelling
Introduction

The development and application of distribution models based on species-habitat or species-environment relationships in ecology has increased in recent years (eg. Walker, 1990; Buckland and Elston, 1993; Augustin et al., 1996; Boroski et al., 1996; Beard et al., 1999; Macdonald et al., 2000; Coops and Catling, 2002; Redfern et al. 2006), in part driven by the need to understand the potential impacts of climate change (Araújo et al., 2005, White and Kerr, 2006, Araújo and New, 2007, Nunes et al., 2007). Determining the relationship between species and their breeding habitat can be particularly important because their populations could be regulated by space limitation (Kokko et al., 2004; Franco et al., 2005; Soutullo et al., 2006). This has been observed for some colonial breeding species (eg. the common guillemot Uria aalge, Kokko et al., 2004), where new recruits are restricted to sub-optimal habitat and this results in lowered breeding success, dispersal, or failure to breed. As breeding is often synchronous or semi-synchronous (within a few weeks) for colonial breeders, suitable habitat becomes occupied over time and habitat availability changes both directly and indirectly as a consequence of the presence of conspecifics. Not only does the presence of an individual in a suitable location render that location unavailable to others, but it may also reduce the suitability of surrounding habitat because of aggressive interactions (Soutullo et al., 2006). As a result of these changes in habitat availability over time, the temporal aspect of habitat choice needs to be considered explicitly (Arthur et al., 1996). However, these dynamic responses have rarely been studied in detail (Guisan and Zimmerman, 2000).
The British population of the grey seal (*Halichoerus grypus*), a colonial breeding mammal, shows clear evidence of resource limitation (SCOS, 2006). Breeding around Britain occurs between the months of August and December, generally on uninhabited, offshore islands. Within a colony, females aggregate when they come ashore. Once a female has found a suitable pupping site, she gives birth to a single white-coated pup and stays with it for a lactation period of 17-20 days. The British grey seal population has been monitored almost every year for the last 4 decades using aerial surveys of these breeding colonies. In 2006 the total population was estimated to be between 97,000 and 159,000 individuals (SCOS 2006). Until 1996 the population had been increasing at an annual rate of between 5-6%, but between 1997 and 2001 the rate fell to 2.8%. It continued to fall to 1.3% between 2001 and 2005, suggesting that population growth was being regulated through some density-dependent process (SCOS, 2006).

Matthiopoulos et al. (2005) distinguished two spatial scales of density dependence: local and global. Local density dependence relates to limiting factors within a colony, such as the number of potential pupping sites, whereas global density dependence relates to factors outwith the colony, such as food availability. It is unknown whether the British grey seal population is being regulated by local or global factors, or by both factors acting simultaneously, although Harwood and Prime (1978) suggested that the ultimate size of a local grey seal population is determined by the number of potential pupping sites within the colony. Pupping sites are locations within the colony that are of the required size and preferred habitat for an individual female to give birth and successfully raise a pup. The ability to identify potential pupping sites
and to predict when they are likely to be occupied is, therefore, essential for the
development of robust management plans for this species.

The factors involved in determining suitable breeding habitat have been investigated
for a number of different species (eg. Bian et al., 1997; Ribe et al., 1998; Howell et
al., 2000; Lawler and Edwards, 2002). For the grey seal, a small number of Scottish
breeding colonies have been intensively studied, and this has resulted in numerous
qualitative descriptions of the environmental factors that females may use when
selecting a pupping site at these colonies (Boyd et al., 1962; Prime, 1981; Anderson
and Harwood, 1985; Pomeroy et al., 1994; Caudron, 1995; Pomeroy et al., 2000).

Access to water - either the sea or pools of freshwater - seems to be particularly
important. Breeding grey seals often aggregate around gullies that provide access to
the sea and around inland pools (Anderson et al., 1975; Pomeroy et al., 1994; Twiss et
al., 2000a; Redman et al., 2001). Seals that are not immediately next to a water
source make regular trips to and from pools of water or the sea (Twiss et al., 2000a;
Redman et al., 2001). The influence of water has been quantified at two colonies, the
Isle of May and North Rona by Twiss et al. (2000a, 2001). Twiss et al. (2001) found
that 2m square cells occupied by breeding females at the Isle of May, Scotland, were
closer to access points to the sea and to pools of water than unoccupied cells, and
predicted that a preference for close proximity to water may restrict colony expansion.

Social factors may also play a role in habitat choice because breeding females have
been observed to respond to conspecifics in ways that could regulate density
(Anderson et al., 1975; Boness et al., 1982; Kovacs, 1987; Caudron, 1998; Pomeroy
et al., 2000). Therefore it is important that such mechanisms are incorporated into any
predictive model of grey seal distribution. Although females aggregate when they
come ashore, they are intolerant of conspecifics that approach closer than 2 body
lengths once they have given birth (Boness et al., 1982; Caudron, 1998; Pomeroy et
al., 2000). This intolerance often leads to aggression. Such aggressive interactions
may serve as a pup protection mechanism: a female is more likely to threaten an
approaching female if her pup is between her and the approaching female than if it is
not (Boness et al., 1982). However, aggression may also set an upper limit to the
density within a colony and it is likely that the spatial distribution of aggressiveness
affects a pregnant female’s decision on where to give birth. Potential levels of
aggression at a particular site will vary dynamically during the breeding season.

Spatially-explicit simulation models are regularly used to investigate different
scenarios for colonisation, species spread and range-shift (eg. Higgins et al., 2001;
MacDonald and Rushton, 2003; Hammershøj et al., 2006, McInerny et al., 2007).
Similar models have considerable potential for simulating the way in which grey seals
establish new colonies and spread across them. The development of such a model,
however, requires quantitative information on the suite of factors that could influence
habitat choice. Twiss et al. (2000a, 2001) quantified the effect of topographical
factors on the average distribution of seals over the entire breeding season. However,
grey seal distribution within a colony varies dynamically over the course of the
pupping season, and this is likely to affect preference. For example, the breeding
season in each colony lasts about 7-8 weeks, but individual females only stay ashore
for 17-20 days. As a result, local densities of seals change on a daily basis as new
females arrive and others leave. Some of the topographical characteristics of a colony
(eg. water availability due to precipitation) also change over the course of the breeding season.

We used a combination of iterative model fitting and individual-based simulations to develop a spatially- and temporally-explicit model of the distribution of breeding grey seals that could be used to predict the effects of an increase in population size or changes in habitat availability at any colony. Because it is impracticable to carry out detailed studies on the ground at all colonies, we chose sets of explanatory variables that could be measured from the photographs that form the basis of the annual surveys of grey seal abundance in the UK. We modelled the occurrence of aggression as a function of topography and the distribution of white-coated pups, and we modelled the locations of newborn pups as a function of topography, the distribution of white-coated pups and aggression. We then investigated how these two models describe the evolution of the spatial distribution of pups during a breeding season using a dynamical individual-based simulation model. Our aim was to identify the most important areas for current breeding requirements, the areas most likely to be colonised during expansion, and how any population regulation through local density dependence might occur.

**Materials and methods**

**STUDY SITE**

The Isle of May (56° 11’N, 2° 33’W) lies off the east coast of Scotland at the mouth of the Firth of Forth. Until the 1970’s very few pups were born on the island, but
production has increased markedly since then and in 2005 had risen to more than
2000 pups (SCOS, 2006).

Behavioural observations were carried out on a geographically discrete gully (approx
0.0016km$^2$), on the east side of the island where pup production was approximately 90
pups in 2000. Observations were carried out on almost all days between 30 October
and 30 November 2000. On average, 6 hrs per day were spent in a hide overlooking
the breeding colony. At the start of each observation period the positions of all the
animals and pools of water were mapped onto an acetate sheet attached to an enlarged
colour photocopy of an aerial photograph of the study site. Pups were classified into
one of the five developmental stages identified by Boyd et al. (1962): stage 1 to 3
pups have white natal coats, during stage 4 pups start to moult, by stage 5 they are
fully moulted and are usually weaned. Information on the location of stage 4 and 5
pups and adult males and females was not included in the analysis because they
frequently change their positions within a colony and their locations do not reflect
where they were born in the case of pups, or where they chose to give birth in the case
of adult females. Continuous scanning of the colony was carried out throughout the
observation period and the time and position of all aggressive interactions (which
encompassed open mouth threats, “flippering” with fore-flipper, wailing
vocalisations, abrupt movements, lunging and biting) were recorded. On return from
fieldwork the daily maps were entered into ArcView 3.2 GIS software.

MODELLING OCCURRENCE OF AGGRESSIVE INTERACTIONS

The locations of all pups in stages 1 to 3 were converted into a 2m x 2m
presence/absence grid. The response variable was defined as the proportion of 2m x
2m cells in a particular habitat category in which aggressive encounters were observed on a particular day. Habitat categories were defined by the distance of the cell from access to the sea (in 10m increments) and from water (10m increments), by its slope (10 degree increments), by the mean number of neighbouring pups (0.1 increments), and by pup presence (0 or 1). On each day, every cell was classified into a habitat category in a multi-dimensional contingency table. This made it possible to calculate the total number (availability) of 2m x 2m cells in each category.

To avoid having to account for variable observation effort, only the 15 days for which there was exactly 6 hrs of observation time were included in the modelling of aggressive interactions. The resulting dataset spanned the observation period, so it was assumed that any temporal trends in aggressive behaviour would be captured by the model.

To take account of the potential effect of local pup density on the occurrence of aggression in a particular cell, the mean number of white-coated pups in the eight neighbouring cells was calculated.

Topographical variables were calculated using an Ordnance Survey Land-Form Profile Digital Elevation Model (DEM) of the study site. A 2m x 2m resolution slope surface was interpolated from the DEM. The distance of every cell from access to the sea and from water on each day was then calculated using the Pathdistance function of ArcInfo 8.1, which takes account of the elevation and slope differences between two points in the calculation of distance (Twiss et al., 2000a).
Some pups were already present on the first observation day, and it was therefore necessary to estimate when the first birth had occurred. This was done by fitting a spline to the daily pup counts plotted against day of the breeding season, assuming that no pups were born prior to 27 September 2000 or after 1 January 2001. Day 1 of the breeding season was estimated to be 13 October 2000, so 30 October (the first day of the observation study) was day 18 of the breeding season (Fig. 1). The predicted number of pups for each day was rounded to the nearest integer. The number of pups born on a given day was calculated as the difference between the number of white coated pups present on that day and the number present on the previous day, plus the number of pups that began moulting on that day (Fig. 1).

A Generalised Additive Model (GAM) (Hastie and Tibshirani, 1990) was fitted to the data (Fig. 2) with a binomial error distribution and logit link function. In the model definition, each habitat category was weighted by its availability. Each explanatory variable was included in the model firstly as a linear term and then as a smooth function. A variable was only included as a smooth function if the improvement in fit, determined by the Un-Biased Risk Estimator (UBRE) score and the percentage deviance explained, outweighed the increase in the number of effective degrees of freedom used to fit the model.

MODELLING THE DISTRIBUTION OF NEWBORN PUPS

In this analysis, the response variable was defined as the proportion of 2m x 2m cells in each habitat type that contained a newborn pup. The cell-by-cell values of aggression for each day predicted by our first model were incorporated as an additional explanatory variable. All days for which data were available on consecutive
days \((n=12)\) were included in the model, not only those with 6 hrs of observation, because the number of newborn pups recorded each day was independent of observation effort. The other explanatory variables were the same as those used to predict aggressiveness. Habitat categories were redefined to include the probability of aggression \((\text{in 0.25 increments})\). Habitat categories on day \(t\) were used to predict newborn pup positions on day \((t+1)\), because grey seal mothers tend to investigate suitable sites on several days before giving birth (Burton et al., 1975).

A quasibinomial GAM was fitted to the data (Fig. 2) with a logit link function, to account for overdispersion in the residuals. The model was weighted by the number of cells present in each habitat category. As before, variables were retained in the model as smooth functions or linear terms depending on their contribution to model fit. As a quasi model was fitted in this case, the Generalized Cross Validation (GCV) score was used along with percentage deviance explained to determine model fit.

SIMULATING PUP DISTRIBUTION OVER THE BREEDING SEASON

For the simulation model to be transferable to other colonies where no data on aggressive interactions or daily pup numbers or distributions are available, the input data has to be extracted from aerial surveys. At least three or four aerial surveys of each colony are carried out annually, providing a series of snapshots of the distribution of pups at different stages of the season. To replicate this process with our observations we used the distribution of pups on the first day of observation \((30\ October\ 2000)\) as the starting point of the simulation. Three observation “survey” days \((6\ November, 17\ November\ and\ 27\ November\ 2000)\) were chosen to provide
To provide the simulation model with a continuous estimate of pup production we used the number of pups born on each day predicted by the same spline we had previously used to estimate the first day of the breeding season (Fig. 1). Fitting such splines to three or four pup counts is carried out routinely as part of the annual assessment of grey seal pup production (SCOS 2006).

GENERATING PUP DISTRIBUTIONS

The distribution of pups observed on the first survey (30 October 2000) was used to seed the simulation and this, along with the topographic information and the GAM fitted to newborn pup locations, was used to predict the probability that a pup would be born in each cell on the following day (Fig. 3). The estimated number of pups born on that day was allocated randomly among the available cells using a weighting based on the predicted probability that a pup would be born in each cell. Each pup was assigned a time-to-moult by selecting at random from a sample of 36 observations of this variable (Redman, pers comm.) and pups were removed from the distribution once they had reached their assigned time-to-moult. The mean number of neighbouring pups each day was calculated based on the new pup distribution. This process was repeated until the end of the breeding season. The positions of pools of water within the colony (and therefore the distance to water surface) changed over the course of the breeding season because of rainfall. It is not possible to track the changes in the distribution of pools between aerial surveys, so the distribution of pools on a particular day was assumed to be the same as that recorded in the previous
survey date until half the total rainfall recorded between surveys had fallen, at which point it was updated to the distribution observed on the next survey.

COMPARISON OF SIMULATED AND NULL MODEL PERFORMANCE

Dynamic models based on GAMs, such as the one developed here, are relatively new. To ensure that such complexity is necessary when modelling a particular species-habitat relationship, the performance of the complex model should be compared with a simpler model. We therefore compared our model’s predictions with a null, uniform probability model. This assumed that a pup could be observed at any location within the study site with equal probability, using the same spatial boundaries of the study site as used by the GAM models. We generated multiple realisations of the processes described by the two models and recorded their spatial predictions at the dates of the three surveys. This was repeated 1,500 times to generate a relative frequency of occupancy for each cell under each model. The first day of the observation study was used as the initial distribution. The log-likelihood of the observed pup distribution occurring under each model was calculated by summing the logarithms of the probability values for all occupied cells. Because probabilities were obtained as relative frequencies via a finite number of simulations, the spatial probability distributions derived from both models always included a large number of cells with zero frequencies. On some surveys some of these cells were, in fact, occupied. This caused a problem with the estimation of log-likelihoods. To allow log-likelihood values to be calculated but still penalise models for underestimating the probability of occupancy, the zero probabilities were replaced by a probability that was lower than any (non-zero) probability generated by either model. The choice of what this value should be is arbitrary, so we repeated our entire analysis 200 times using values...
between $6 \times 10^{-5}$ and $8.2 \times 10^{-30}$. In each case, the values for each cell were rescaled so
that the estimated probabilities for all space summed to one. Since the two models had
different numbers of parameters we used Akaike’s Information Criterion (AIC) to
penalise the log-likelihood associated with each model by the number of parameters.
We compared the values of the AIC from the two models for each survey date.

Results

OCCURRENCE OF AGGRESSIVE INTERACTIONS

Aggressive interactions were observed throughout the breeding season and occurred
predominantly in cells with a slope of $25^\circ$ or less that were near to water. They were
seldom observed in cells with pups, but were more frequent in cells whose
neighbouring cells contained a pup. There was a non-linear relationship between
aggression and the distance from access to the sea whereby the probability of
aggression occurring increased up to 30m from the access point and then decreased.
The best-fitting GAM retained all of the variables with distance to water, distance to
access and day included as smooth functions and slope, presence of pups and
neighbouring pups as linear terms (Table 1). The probability of aggression was
predicted to decrease with increasing distance to water and day and increase with
distance to access, slope, number of neighbours and pup presence (Table 1). The
model explained 51.5% of the deviance.

DISTRIBUTION OF NEWBORN PUPS
From the data it was noted that newborn pups were found close to access to the sea, but less often within the first 10m from the access point. They were generally close to water sources, on slopes up to 25°, in cells with other pups present and with pups in neighbouring cells. More pups appeared to be born in habitats with a low probability of aggression. Few pups were born after day 20.

Aggression was significant in the fitted GAM but when compared with a simpler model without aggression as a variable, it did not appear to improve the overall fit of the model (25.5% deviance explained compared with 25% deviance explained). These two models were compared further to investigate the role of aggression in predicting the spatial distribution of pups relative to a null model. Both models also retained distance to water, distance to access, mean number of neighbouring pups and day (Table 2). The probability of a pup being born in a particular habitat category decreased with distance to water, the probability of aggression and day of the breeding season and increased with distance to access and the mean number of neighbouring pups (Table 2).

COMPARISON OF OBSERVED, SIMULATED AND UNIFORM DISTRIBUTIONS

Under the simulation model that incorporated the GAM without aggression, the cells with the highest probability of occupancy on the second survey date were those surrounding the cells that contained pups on the first survey date (Fig. 4). This was less pronounced under the simulation that incorporated the GAM with aggression. Relatively high probabilities of occupancy were predicted under both models (with and without aggression) towards the inland area of the study site, but this did not fully
account for the observed increase in this area, in particular at the furthest inland points of the study area. A similar pattern was seen on the third and fourth survey dates, although the probabilities under the simulation models are more diffuse in the centre of the study area particularly for the simulation model with aggression and again, there is less spread inland under both models than was observed (Fig. 4). The null model of uniform distribution showed no resemblance to the observed pup distribution (Fig. 4).

COMPARISON OF SIMULATED AND NULL MODEL PERFORMANCE
On all three survey dates the AIC values suggest that the observed distribution is more likely to occur under the conditions of the null model as compared to either simulation model. The observations on all three survey dates had the lowest likelihood of occurring under the simulation model that incorporated the GAM with aggression, as measured by AIC, across all replacement probabilities (Table 3).

Discussion
Modelling habitat preference in a dynamic, density-dependent context requires that the effects of both spatial and temporal variability be taken into consideration. At our study site, environmental change during the breeding season had a clear effect on habitat choice. Although most of the topographical features of the study site did not change during the course of the study period, the distance an animal had to travel to get to a pool of water declined over time. A similar process should occur at most breeding colonies in the UK, because precipitation tends to increase between the months of August and December, creating additional pools of water and enlarging existing ones.
The number of animals present in different habitat categories also changed over time. The first females that arrived at the study site gave birth close to the access gully, although rarely within the first 10m. Towards the middle of the observation period, which coincided with the greatest number of white-coated pups on the study site, many pups were born up to 100m away from the access point. A similar progression towards inland pupping sites has been observed in other studies (Anderson et al., 1975; Kovacs, 1987; Twiss et al., 2000a, 2001). Towards the end of the observation period there were few white-coated pups left on the colony. However, the majority of these were more than 30m from the access point, implying that late-arriving females had not occupied the sites close to access made available by the departure of females that had pupped early in the season.

The inclusion of day as a smooth function in the aggressiveness model indicates that temporal trends in the occurrence of aggression are not linear. The locations and frequency of aggressive encounters changed over time because of the changing locations and numbers of females. The positive relationship between aggression and pup presence in both the same and neighbouring cells supports the suggestion that aggression is a pup protection mechanism (Boness et al., 1982; Caudron, 1998). As a result, more aggressive encounters were recorded inland later in the observation period. However, aggressive encounters between females, and females and males, were also recorded in locations where pups were not present. These mainly involved individuals travelling to and from water, or females fighting for space close to water.
Aggressive encounters were most frequent between 20m and 60m from the access to the sea. Few encounters occurred within the first 10m from access, which explains the unexpected positive relationship between distance to access and occurrence of aggression. The only access to the sea from the study site is via a narrow, steep-sided gully. As a result, the access point was often congested with females moving to and from the sea. This may be why very few pups were born close to the access gully and low levels of aggression were recorded there. The risk of separation or injury to pups born in this area would have been high.

The highly significant negative relationship between aggression and distance to water indicates that most aggressive encounters occurred close to the freshwater pools. Many females visited the inland pools on a regular basis, rather than go to the sea. Previous studies have shown that females prefer pupping sites close to an access point to the sea or close to inland pools of water (Twiss et al., 2000a, 2001). Access to water is thought to be important for thermoregulation, because keeping the body wet may assist in controlling body temperature (Anderson et al., 1975), and possibly for drinking (Twiss et al., 2002). In areas where there are few pupping sites close to the sea, access to freshwater pools may be sufficient to allow females to stay cool and the costs for a female visiting these pools, in terms of energy expended on travelling to and from water, aggressive interactions with neighbours, harassment by males and separation from her pup (Boness et al., 1995), are likely to be lower than those incurred in travelling to the sea.

The relationship between distance to water and the positions of newborn pups was as expected, with pups being born close to water sources. The quantification of this
relationship between water and pupping sites is important because this is a feature
which appears to be paramount to the maintenance and expansion of colonies, yet it is
likely to alter as a result of climate change, agriculture or other anthropogenic
manipulations of the landscape. Conversely, the model predicted that the probability
of a pup being born in a cell would increase with distance to access. This relationship
is probably an artefact of the topography of the study site, where there was heavy
traffic close to the sole access point. This situation is unusual, and reduces the general
applicability of the model developed here.

The role of aggression in the prediction of newborn pup locations was interesting
because although there was a significant negative relationship between predicted
levels of aggression and newborn pup locations, it did not improve either model fit or
the resulting spatial predictions. The negative relationship between aggression and
newborn pup locations implies that there is an energetic cost to females of giving birth
in locations where the probability of aggressive interactions is high. However, there
is a contradiction in the newborn pup model given the results from the aggression
model, whereby there is a negative relationship between newborn pup location and
distance to water alongside a negative relationship between newborn pup location and
probability of aggression. Similarly, there is a positive relationship between newborn
pup location and mean number of neighbouring pups alongside the negative
relationship with aggression. Therefore, females are giving birth close to water and
close to other pups relative to the range of habitat that is available, but not so close
that aggression is at its highest. We know from the aggression model that aggression
increases near water sources and in the vicinity of other pups but the negative
relationship with newborn pup location suggests that some compromise is reached
between attraction to pools and conspecifics and the cost of aggression. However, as
the inclusion of aggression as a variable does not improve model fit or greatly alter
the spatial predictions from the model, it would appear that distance to water and
presence of neighbouring pups are the over-riding predictors in the newborn pup
model. Given this and the requirement for parsimony, it would seem appropriate in
most situations to select the newborn pup model without aggression over the model
with aggression. However, it may be that on colonies where resources are more
limiting and/or seal numbers are much higher there is a role for the model that
includes aggression, as observed distributions may only be explained by the inclusion
of a density-regulating mechanism close to the water sources. This could be
investigated on colonies thought to be close to carrying-capacity, where the numbers
of pups born each year has reached a plateau.

There are many other behavioural or social characteristics of a grey seal breeding
colony that may affect a female’s decision of where to give birth. For example, female
grey seals demonstrate both site fidelity and philopatry which could give rise to a
complex social structure based on groups of maternally-related females within a
colony (Pomeroy et al., 2000). The Isle of May was only colonised in the 1970’s and
our study site has only been used since the late 1990’s. Newly colonised breeding
colonies are likely to be occupied by younger females who are unable to compete for
space in their natal breeding colony. One of the advantages of our study site was that
the effects of matrilineal social organisation were likely to be minimal. Therefore, the
site choices observed in this study were more likely to be based on topography and the
presence of conspecifics than on complex social factors. This is a useful feature of
the model because we are interested in how the distribution of seals might expand as
the population increases. Because of the effects of site fidelity, younger females are most likely to be involved in this process.

The predictive capability of regression models such as GAMs is generally low due to the complex way empirical data are incorporated (Power, 1993; Roloff and Kernohan, 1999; Guisan and Zimmermann, 2000; Pearce and Ferrier, 2000; Guisan et al., 2002). A problem specific to the extrapolation of the relationships observed at our study site to other colonies is that, although we have taken habitat availability into account, selection for a particular habitat within a colony may be dependent on the relative availability of other habitat types and this will vary between colonies (Boyce and McDonald, 1999; Mysterud and Ims, 1999).

In this study, the spatiotemporal simulation of pupping site selection demonstrated that a newborn pup model and information on pup distribution close to the start of the breeding season produced subsequent distributions of pups that, at least visually, appeared better than a null model. The inability of the simulation model to outperform the null model when assessed using likelihood and AIC was partly a result of differences in the observed and predicted distributions, but was also a result of the high penalty incorporated into the AIC calculation for the simulation model to account for the effective degrees of freedom used by the GAM. Under the null model there was a probability of occurrence in all cells that were observed to contain a pup, a result not matched by the simulation model.

The better performance of the null model when compared with the simulation model implies that the entire study area was suitable for pupping and that there was little
selection of particular habitat types within the boundaries of the study site (up to
100m from water and 110m from access to the sea), so at the scale of the study area
there seems little advantage of predicting pupping site location using a complex
dynamic model. The drawback of the null model is that it is unlikely to apply over
larger scale areas and it is unlikely that we could extrapolate the assumption of equal
suitability to larger distances from water or access. The GAM models however are
biologically informative and provide us with an insight into the energetic trade-offs
that are apparent in a female's choice of pupping site, and therefore may be more
applicable to larger scale study sites or to extrapolation beyond the boundaries of the
environmental characteristics observed in the modelled study site. Both the simple
rules resulting from the null model and the more complex relationships resulting from
the GAM models can be used as part of the process of evaluating whether
management actions will ensure a favourable conservation status for grey seals. For
example, the impact of different management practices and climate change on the
topographical characteristics of grey seal colonies, particularly the distribution of
water, can be investigated. The consequences of these changes for the distribution
and abundance of grey seals within colonies can then be analysed using the models
we developed here.
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Table 1: Output of a GAM fitted to the daily occurrence of aggressive interactions between grey seal adults at the study site on the Isle of May during the 2000 breeding season. DW = Distance to water, DA = Distance to access, S = Slope, NP = Neighbouring pups, PP = Pup presence, Day = Day.

| Linear Terms | Coefficient estimate | Z value | Pr(>|Z|) |
|--------------|----------------------|---------|---------|
|              |                      |         | <0.001 *** |
|              |                      |         | <0.01 **  |
|              |                      |         | <0.05*   |
| S            | 0.031                | 4.99    | ***      |
| NP           | 13.26                | 27.39   | ***      |
| PP           | 2.19                 | 17.52   | ***      |

<table>
<thead>
<tr>
<th>Smooth Functions</th>
<th>Effective degrees of freedom</th>
<th>Chi-square value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>DW</td>
<td>5.21</td>
<td>440.00</td>
<td>***</td>
</tr>
<tr>
<td>DA</td>
<td>8.16</td>
<td>214.60</td>
<td>***</td>
</tr>
<tr>
<td>DAY</td>
<td>7.77</td>
<td>125.60</td>
<td>***</td>
</tr>
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</table>
Table 2: Output of a GAM fitted to the daily locations of newborn grey seal pups at the study site on the Isle of May during the 2000 breeding season (a) with predicted aggression included as a variable, (b) without predicted aggression. 

$\text{DW} = \text{Distance to water}, \text{DA} = \text{Distance to access}, \text{NP} = \text{Neighbouring pups}, \text{AGG} = \text{Aggression}, \text{Day} = \text{Day}.$

(a)

| Linear Terms | Coefficient estimate | T value | Pr(>|T|) |
|--------------|----------------------|---------|----------|
|              |                      |         | <0.001 ***<0.01 **<0.05* |
| DW           | -0.10                | -12.11  | ***      |
| NP           | 9.15                 | 13.26   | ***      |
| AGG          | -2.22                | -3.16   | **       |

| Smooth Functions | Effective degrees of freedom | F value | P-value(>|F|) |
|------------------|-------------------------------|---------|--------------|
|                  |                               |         | <0.001 ***<0.01 **<0.05* |
| DA               | 7.67                          | 25.36   | ***         |
| DAY              | 8.54                          | 21.82   | ***         |

(b)

| Linear Terms | Coefficient estimate | T value | Pr(>|T|) |
|--------------|----------------------|---------|----------|
|              |                      |         | <0.001 ***<0.01 **<0.05* |
| DW           | -0.10                | -12.53  | ***      |
| NP           | 7.66                 | 13.98   | ***      |

| Smooth Functions | Effective degrees of freedom | F value | P-value(>|F|) |
|------------------|-------------------------------|---------|--------------|
|                  |                               |         | <0.001 ***<0.01 **<0.05* |
| DA               | 7.41                          | 26.85   | ***         |
| DAY              | 8.60                          | 25.41   | ***         |
Table 3: Akaike Information Criteria (AIC) values for the likelihood of observed grey seal pup distributions occurring under the simulation models with and without aggression and the null model on surveys 2, 3 and 4. Values shown represent likelihoods derived when the upper- and lower-most replacement probabilities were incorporated. Lower AIC values indicate a better model fit.

<table>
<thead>
<tr>
<th>Survey</th>
<th>Upper replacement probability</th>
<th>Lower replacement probability</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Simulation with aggression</td>
<td>Simulation without aggression</td>
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<tr>
<td>Survey 2</td>
<td>712.75</td>
<td>691.29</td>
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<td>Survey 3</td>
<td>676.65</td>
<td>664.94</td>
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<tr>
<td>Survey 4</td>
<td>346.93</td>
<td>355.98</td>
</tr>
</tbody>
</table>
Figure Legends

Figure 1: The spline fitted to the numbers of pups present on observation days (black squares), the calculated number of births each day of the breeding season based on the number of pups present on that day and the number present on the previous day, plus the number that began moulting on that day (grey circles), and the cumulative birth curve (black triangles) over the duration of the breeding season.

Figure 2: Schematic describing the relationships between the GAMs and the data sources.

Figure 3: Schematic describing the role of the GAMs and the data sources in the individual-based models. The dashed lines represent data sources that are involved only in the first iteration of the individual-based models.

Figure 4: The (a) observed, (b) simulated with aggression, (c) simulated without aggression and (d) null grey seal pup distributions on surveys 2, 3 and 4. The legend only corresponds to the simulated and null distributions. In the observed distributions, black = 0 pups, grey = 1 pup, white = 2 pups.
Fig. 1
GAM predicting number of aggressive interactions

Topographic information from GIS

GAM predicting location of newborn pups

Observed number of newborn pups

Observed distribution of older pups

Fig. 2
GAM predicting number of aggressive interactions

Topographic information from GIS

Observed distribution of older pups in first aerial survey

GAM predicting location of newborn pups

Predicted number of newborn pups on current day from birth curve

Predicted distribution of pups on next day

Fig. 3