

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

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1 **Abstract**

2

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

21

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

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1 **Introduction**

2

3 The development and application of distribution models based on species-habitat or
4 species-environment relationships in ecology has increased in recent years (eg
5 Walker, 1990; Buckland and Elston, 1993; Augustin et al., 1996; Boroski et al., 1996;
6 Beard et al., 1999; Macdonald et al., 2000; Coops and Catling, 2002; Redfern et al.
7 2006), in part driven by the need to understand the potential impacts of climate
8 change (Araújo et al., 2005, White and Kerr, 2006, Araújo and New, 2007, Nunes et
9 al., 2007). Determining the relationship between species and their breeding habitat
10 can be particularly important because their populations could be regulated by space
11 limitation (Kokko et al., 2004; Franco et al., 2005; Soutullo et al., 2006). This has
12 been observed for some colonial breeding species (eg. the common guillemot *Uria*
13 *aalge*, Kokko et al., 2004), where new recruits are restricted to sub-optimal habitat
14 and this results in lowered breeding success, dispersal, or failure to breed. As
15 breeding is often synchronous or semi-synchronous (within a few weeks) for colonial
16 breeders, suitable habitat becomes occupied over time and habitat availability changes
17 both directly and indirectly as a consequence of the presence of conspecifics. Not
18 only does the presence of an individual in a suitable location render that location
19 unavailable to others, but it may also reduce the suitability of surrounding habitat
20 because of aggressive interactions (Soutullo et al., 2006). As a result of these changes
21 in habitat availability over time, the temporal aspect of habitat choice needs to be
22 considered explicitly (Arthur et al, 1996). However, these dynamic responses have
23 rarely been studied in detail (Guisan and Zimmerman, 2000).

24

1 The British population of the grey seal (*Halichoerus grypus*), a colonial breeding
2 mammal, shows clear evidence of resource limitation (SCOS, 2006). Breeding
3 around Britain occurs between the months of August and December, generally on
4 uninhabited, offshore islands. Within a colony, females aggregate when they come
5 ashore. Once a female has found a suitable pupping site, she gives birth to a single
6 white-coated pup and stays with it for a lactation period of 17-20 days. The British
7 grey seal population has been monitored almost every year for the last 4 decades
8 using aerial surveys of these breeding colonies. In 2006 the total population was
9 estimated to be between 97,000 and 159,000 individuals (SCOS 2006). Until 1996 the
10 population had been increasing at an annual rate of between 5-6%, but between 1997
11 and 2001 the rate fell to 2.8%. It continued to fall to 1.3% between 2001 and 2005,
12 suggesting that population growth was being regulated through some density-
13 dependent process (SCOS, 2006).

14

15 Matthiopoulos et al. (2005) distinguished two spatial scales of density dependence:
16 local and global. Local density dependence relates to limiting factors within a colony,
17 such as the number of potential pupping sites, whereas global density dependence
18 relates to factors outwith the colony, such as food availability. It is unknown whether
19 the British grey seal population is being regulated by local or global factors, or by
20 both factors acting simultaneously, although Harwood and Prime (1978) suggested
21 that the ultimate size of a local grey seal population is determined by the number of
22 potential pupping sites within the colony. Pupping sites are locations within the
23 colony that are of the required size and preferred habitat for an individual female to
24 give birth and successfully raise a pup. The ability to identify potential pupping sites

1 and to predict when they are likely to be occupied is, therefore, essential for the
2 development of robust management plans for this species.

3

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

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

21

22 Social factors may also play a role in habitat choice because breeding females have
23 been observed to respond to conspecifics in ways that could regulate density
24 (Anderson et al., 1975; Boness et al., 1982; Kovacs, 1987; Caudron, 1998; Pomeroy
25 et al., 2000). Therefore it is important that such mechanisms are incorporated into any

1 predictive model of grey seal distribution. Although females aggregate when they
2 come ashore, they are intolerant of conspecifics that approach closer than 2 body
3 lengths once they have given birth (Boness et al., 1982; Caudron, 1998; Pomeroy et
4 al., 2000). This intolerance often leads to aggression. Such aggressive interactions
5 may serve as a pup protection mechanism: a female is more likely to threaten an
6 approaching female if her pup is between her and the approaching female than if it is
7 not (Boness et al., 1982). However, aggression may also set an upper limit to the
8 density within a colony and it is likely that the spatial distribution of aggressiveness
9 affects a pregnant female's decision on where to give birth. Potential levels of
10 aggression at a particular site will vary dynamically during the breeding season.

11

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

1 (eg. water availability due to precipitation) also change over the course of the
2 breeding season.

3

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

19

20 **Materials and methods**

21

22 STUDY SITE

23 The Isle of May ($56^{\circ} 11'N$, $2^{\circ} 33'W$) lies off the east coast of Scotland at the mouth of
24 the Firth of Forth. Until the 1970's very few pups were born on the island, but

1 production has increased markedly since then and in 2005 had risen to more than
2 2000 pups (SCOS, 2006).

3

4 Behavioural observations were carried out on a geographically discrete gully (approx
5 0.0016km²), on the east side of the island where pup production was approximately 90
6 pups in 2000. Observations were carried out on almost all days between 30 October
7 and 30 November 2000. On average, 6 hrs per day were spent in a hide overlooking
8 the breeding colony. At the start of each observation period the positions of all the
9 animals and pools of water were mapped onto an acetate sheet attached to an enlarged
10 colour photocopy of an aerial photograph of the study site. Pups were classified into
11 one of the five developmental stages identified by Boyd et al. (1962): stage 1 to 3
12 pups have white natal coats, during stage 4 pups start to moult, by stage 5 they are
13 fully moulted and are usually weaned. Information on the location of stage 4 and 5
14 pups and adult males and females was not included in the analysis because they
15 frequently change their positions within a colony and their locations do not reflect
16 where they were born in the case of pups, or where they chose to give birth in the case
17 of adult females. Continuous scanning of the colony was carried out throughout the
18 observation period and the time and position of all aggressive interactions (which
19 encompassed open mouth threats, “flippering” with fore-flipper, wailing
20 vocalisations, abrupt movements, lunging and biting) were recorded. On return from
21 fieldwork the daily maps were entered into ArcView 3.2 GIS software.

23 MODELLING OCCURRENCE OF AGGRESSIVE INTERACTIONS

24 The locations of all pups in stages 1 to 3 were converted into a 2m x 2m
25 presence/absence grid. The response variable was defined as the proportion of 2m x

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

8

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

14

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

18

19 Topographical variables were calculated using an Ordnance Survey Land-Form
20 Profile Digital Elevation Model (DEM) of the study site. A 2m x 2m resolution slope
21 surface was interpolated from the DEM. The distance of every cell from access to the
22 sea and from water on each day was then calculated using the Pathdistance function of
23 ArcInfo 8.1, which takes account of the elevation and slope differences between two
24 points in the calculation of distance (Twiss et al., 2000a).

25

1 Some pups were already present on the first observation day, and it was therefore
2 necessary to estimate when the first birth had occurred. This was done by fitting a
3 spline to the daily pup counts plotted against day of the breeding season, assuming
4 that no pups were born prior to 27 September 2000 or after 1 January 2001. Day 1 of
5 the breeding season was estimated to be 13 October 2000, so 30 October (the first day
6 of the observation study) was day 18 of the breeding season (Fig. 1). The predicted
7 number of pups for each day was rounded to the nearest integer. The number of pups
8 born on a given day was calculated as the difference between the number of white
9 coated pups present on that day and the number present on the previous day, plus the
10 number of pups that began moulting on that day (Fig. 1).

11

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

20

21 MODELLING THE DISTRIBUTION OF NEWBORN PUPS

22 In this analysis, the response variable was defined as the proportion of 2m x 2m cells
23 in each habitat type that contained a newborn pup. The cell-by-cell values of
24 aggression for each day predicted by our first model were incorporated as an
25 additional explanatory variable. All days for which data were available on consecutive

1 days ($n=12$) were included in the model, not only those with 6 hrs of observation,
2 because the number of newborn pups recorded each day was independent of
3 observation effort. The other explanatory variables were the same as those used to
4 predict aggressiveness. Habitat categories were redefined to include the probability of
5 aggression (in 0.25 increments). Habitat categories on day t were used to predict
6 newborn pup positions on day ($t+1$), because grey seal mothers tend to investigate
7 suitable sites on several days before giving birth (Burton et al., 1975).

8

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

15

16 SIMULATING PUP DISTRIBUTION OVER THE BREEDING SEASON

17 For the simulation model to be transferable to other colonies where no data on
18 aggressive interactions or daily pup numbers or distributions are available, the input
19 data has to be extracted from aerial surveys. At least three or four aerial surveys of
20 each colony are carried out annually, providing a series of snapshots of the
21 distribution of pups at different stages of the season. To replicate this process with our
22 observations we used the distribution of pups on the first day of observation (30
23 October 2000) as the starting point of the simulation. Three observation “survey” days
24 (6 November, 17 November and 27 November 2000) were chosen to provide

1 information on pup distribution that would be equivalent to that obtained from aerial
2 surveys.

3

4 To provide the simulation model with a continuous estimate of pup production we
5 used the number of pups born on each day predicted by the same spline we had
6 previously used to estimate the first day of the breeding season (Fig. 1). Fitting such
7 splines to three or four pup counts is carried out routinely as part of the annual
8 assessment of grey seal pup production (SCOS 2006).

9

10 GENERATING PUP DISTRIBUTIONS

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

1 survey date until half the total rainfall recorded between surveys had fallen, at which
2 point it was updated to the distribution observed on the next survey.

3

4 COMPARISON OF SIMULATED AND NULL MODEL PERFORMANCE

5 Dynamic models based on GAMs, such as the one developed here, are relatively new.
6 To ensure that such complexity is necessary when modelling a particular species-
7 habitat relationship, the performance of the complex model should be compared with
8 a simpler model. We therefore compared our model's predictions with a null, uniform
9 probability model. This assumed that a pup could be observed at any location within
10 the study site with equal probability, using the same spatial boundaries of the study
11 site as used by the GAM models. We generated multiple realisations of the processes
12 described by the two models and recorded their spatial predictions at the dates of the
13 three surveys. This was repeated 1,500 times to generate a relative frequency of
14 occupancy for each cell under each model. The first day of the observation study was
15 used as the initial distribution. The log-likelihood of the observed pup distribution
16 occurring under each model was calculated by summing the logarithms of the
17 probability values for all occupied cells. Because probabilities were obtained as
18 relative frequencies via a finite number of simulations, the spatial probability
19 distributions derived from both models always included a large number of cells with
20 zero frequencies. On some surveys some of these cells were, in fact, occupied. This
21 caused a problem with the estimation of log-likelihoods. To allow log-likelihood
22 values to be calculated but still penalise models for underestimating the probability of
23 occupancy, the zero probabilities were replaced by a probability that was lower than
24 any (non-zero) probability generated by either model. The choice of what this value
25 should be is arbitrary, so we repeated our entire analysis 200 times using values

1 between 6×10^{-5} and 8.2×10^{-30} . In each case, the values for each cell were rescaled so
2 that the estimated probabilities for all space summed to one. Since the two models had
3 different numbers of parameters we used Akaike's Information Criterion (AIC) to
4 penalise the log-likelihood associated with each model by the number of parameters.
5 We compared the values of the AIC from the two models for each survey date.

6

7 **Results**

8

9 OCCURRENCE OF AGGRESSIVE INTERACTIONS

10 Aggressive interactions were observed throughout the breeding season and occurred
11 predominantly in cells with a slope of 25° or less that were near to water. They were
12 seldom observed in cells with pups, but were more frequent in cells whose
13 neighbouring cells contained a pup. There was a non-linear relationship between
14 aggression and the distance from access to the sea whereby the probability of
15 aggression occurring increased up to 30m from the access point and then decreased.

16

17 The best-fitting GAM retained all of the variables with distance to water, distance to
18 access and day included as smooth functions and slope, presence of pups and
19 neighbouring pups as linear terms (Table 1). The probability of aggression was
20 predicted to decrease with increasing distance to water and day and increase with
21 distance to access, slope, number of neighbours and pup presence (Table 1). The
22 model explained 51.5% of the deviance.

23

24 DISTRIBUTION OF NEWBORN PUPS

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

6

7 Aggression was significant in the fitted GAM but when compared with a simpler
8 model without aggression as a variable, it did not appear to improve the overall fit of
9 the model (25.5% deviance explained compared with 25% deviance explained).

10 These two models were compared further to investigate the role of aggression in
11 predicting the spatial distribution of pups relative to a null model. Both models also
12 retained distance to water, distance to access, mean number of neighbouring pups and
13 day (Table 2). The probability of a pup being born in a particular habitat category
14 decreased with distance to water, the probability of aggression and day of the
15 breeding season and increased with distance to access and the mean number of
16 neighbouring pups (Table 2).

17

18 COMPARISON OF OBSERVED, SIMULATED AND UNIFORM 19 DISTRIBUTIONS

20 Under the simulation model that incorporated the GAM without aggression, the cells
21 with the highest probability of occupancy on the second survey date were those
22 surrounding the cells that contained pups on the first survey date (Fig. 4). This was
23 less pronounced under the simulation that incorporated the GAM with aggression.
24 Relatively high probabilities of occupancy were predicted under both models (with
25 and without aggression) towards the inland area of the study site, but this did not fully

1 account for the observed increase in this area, in particular at the furthest inland points
2 of the study area. A similar pattern was seen on the third and fourth survey dates,
3 although the probabilities under the simulation models are more diffuse in the centre
4 of the study area particularly for the simulation model with aggression and again,
5 there is less spread inland under both models than was observed (Fig. 4). The null
6 model of uniform distribution showed no resemblance to the observed pup
7 distribution (Fig. 4).

8

9 COMPARISON OF SIMULATED AND NULL MODEL PERFORMANCE

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

15

16 Discussion

17 Modelling habitat preference in a dynamic, density-dependent context requires that
18 the effects of both spatial and temporal variability be taken into consideration. At our
19 study site, environmental change during the breeding season had a clear effect on
20 habitat choice. Although most of the topographical features of the study site did not
21 change during the course of the study period, the distance an animal had to travel to
22 get to a pool of water declined over time. A similar process should occur at most
23 breeding colonies in the UK, because precipitation tends to increase between the
24 months of August and December, creating additional pools of water and enlarging
25 existing ones.

1

2 The number of animals present in different habitat categories also changed over time.
3 The first females that arrived at the study site gave birth close to the access gully,
4 although rarely within the first 10m. Towards the middle of the observation period,
5 which coincided with the greatest number of white-coated pups on the study site,
6 many pups were born up to 100m away from the access point. A similar progression
7 towards inland pupping sites has been observed in other studies (Anderson et al.,
8 1975; Kovacs, 1987; Twiss et al., 2000a, 2001). Towards the end of the observation
9 period there were few white-coated pups left on the colony. However, the majority of
10 these were more than 30m from the access point, implying that late-arriving females
11 had not occupied the sites close to access made available by the departure of females
12 that had pupped early in the season.

13

14 The inclusion of day as a smooth function in the aggressiveness model indicates that
15 temporal trends in the occurrence of aggression are not linear. The locations and
16 frequency of aggressive encounters changed over time because of the changing
17 locations and numbers of females. The positive relationship between aggression and
18 pup presence in both the same and neighbouring cells supports the suggestion that
19 aggression is a pup protection mechanism (Boness et al., 1982; Caudron, 1998). As a
20 result, more aggressive encounters were recorded inland later in the observation
21 period. However, aggressive encounters between females, and females and males,
22 were also recorded in locations where pups were not present. These mainly involved
23 individuals travelling to and from water, or females fighting for space close to water.

24

1 Aggressive encounters were most frequent between 20m and 60m from the access to
2 the sea. Few encounters occurred within the first 10m from access, which explains the
3 unexpected positive relationship between distance to access and occurrence of
4 aggression. The only access to the sea from the study site is via a narrow, steep-sided
5 gully. As a result, the access point was often congested with females moving to and
6 from the sea. This may be why very few pups were born close to the access gully and
7 low levels of aggression were recorded there. The risk of separation or injury to pups
8 born in this area would have been high.

9

10 The highly significant negative relationship between aggression and distance to water
11 indicates that most aggressive encounters occurred close to the freshwater pools.

12 Many females visited the inland pools on a regular basis, rather than go to the sea.

13 Previous studies have shown that females prefer pupping sites close to an access point
14 to the sea or close to inland pools of water (Twiss et al., 2000a, 2001). Access to
15 water is thought to be important for thermoregulation, because keeping the body wet
16 may assist in controlling body temperature (Anderson et al., 1975), and possibly for
17 drinking (Twiss et al., 2002). In areas where there are few pupping sites close to the
18 sea, access to freshwater pools may be sufficient to allow females to stay cool and the
19 costs for a female visiting these pools, in terms of energy expended on travelling to
20 and from water, aggressive interactions with neighbours, harassment by males and
21 separation from her pup (Boness et al., 1995), are likely to be lower than those
22 incurred in travelling to the sea.

23

24 The relationship between distance to water and the positions of newborn pups was as
25 expected, with pups being born close to water sources. The quantification of this

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

9

10 The role of aggression in the prediction of newborn pup locations was interesting
11 because although there was a significant negative relationship between predicted
12 levels of aggression and newborn pup locations, it did not improve either model fit or
13 the resulting spatial predictions. The negative relationship between aggression and
14 newborn pup locations implies that there is an energetic cost to females of giving birth
15 in locations where the probability of aggressive interactions is high. However, there
16 is a contradiction in the newborn pup model given the results from the aggression
17 model, whereby there is a negative relationship between newborn pup location and
18 distance to water alongside a negative relationship between newborn pup location and
19 probability of aggression. Similarly, there is a positive relationship between newborn
20 pup location and mean number of neighbouring pups alongside the negative
21 relationship with aggression. Therefore, females are giving birth close to water and
22 close to other pups relative to the range of habitat that is available, but not so close
23 that aggression is at its highest. We know from the aggression model that aggression
24 increases near water sources and in the vicinity of other pups but the negative
25 relationship with newborn pup location suggests that some compromise is reached

1 between attraction to pools and conspecifics and the cost of aggression. However, as
2 the inclusion of aggression as a variable does not improve model fit or greatly alter
3 the spatial predictions from the model, it would appear that distance to water and
4 presence of neighbouring pups are the over-riding predictors in the newborn pup
5 model. Given this and the requirement for parsimony, it would seem appropriate in
6 most situations to select the newborn pup model without aggression over the model
7 with aggression. However, it may be that on colonies where resources are more
8 limiting and/or seal numbers are much higher there is a role for the model that
9 includes aggression, as observed distributions may only be explained by the inclusion
10 of a density-regulating mechanism close to the water sources. This could be
11 investigated on colonies thought to be close to carrying-capacity, where the numbers
12 of pups born each year has reached a plateau.

13

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

1 the population increases. Because of the effects of site fidelity, younger females are
2 most likely to be involved in this process.

3

4 The predictive capability of regression models such as GAMs is generally low due to
5 the complex way empirical data are incorporated (Power, 1993; Roloff and Kernohan,
6 1999; Guisan and Zimmermann, 2000; Pearce and Ferrier, 2000; Guisan et al., 2002).
7 A problem specific to the extrapolation of the relationships observed at our study site
8 to other colonies is that, although we have taken habitat availability into account,
9 selection for a particular habitat within a colony may be dependent on the relative
10 availability of other habitat types and this will vary between colonies (Boyce and
11 McDonald, 1999; Mysterud and Ims, 1999).

12

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

23

24 The better performance of the null model when compared with the simulation model
25 implies that the entire study area was suitable for pupping and that there was little

1 selection of particular habitat types within the boundaries of the study site (up to
2 100m from water and 110m from access to the sea), so at the scale of the study area
3 there seems little advantage of predicting pupping site location using a complex
4 dynamic model. The drawback of the null model is that it is unlikely to apply over
5 larger scale areas and it is unlikely that we could extrapolate the assumption of equal
6 suitability to larger distances from water or access. The GAM models however are
7 biologically informative and provide us with an insight into the energetic trade-offs
8 that are apparent in a female's choice of pupping site, and therefore may be more
9 applicable to larger scale study sites or to extrapolation beyond the boundaries of the
10 environmental characteristics observed in the modelled study site. Both the simple
11 rules resulting from the null model and the more complex relationships resulting from
12 the GAM models can be used as part of the process of evaluating whether
13 management actions will ensure a favourable conservation status for grey seals. For
14 example, the impact of different management practices and climate change on the
15 topographical characteristics of grey seal colonies, particularly the distribution of
16 water, can be investigated. The consequences of these changes for the distribution
17 and abundance of grey seals within colonies can then be analysed using the models
18 we developed here.

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1 **Acknowledgements**

2

3 We are grateful to the Sea Mammal Research Unit personnel who were present on the
4 Isle of May in 2000, in particular Paddy Pomeroy and Simon Moss, for their help with
5 aspects of the field study and to Callan Duck and Phil Lovell for assistance in ground-
6 truthing the aerial photographs of the island. We would also like to thank Carmen
7 Fernandez for statistical advice. This work was funded by a Natural Environment
8 Research Council (NERC) studentship to CMS.

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1 Table 1: Output of a GAM fitted to the daily occurrence of aggressive interactions
 2 between grey seal adults at the study site on the Isle of May during the 2000
 3 breeding season. DW = Distance to water, DA = Distance to access, S =
 4 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	***
Smooth Functions	Effective degrees of freedom	Chi-square value	P-value
			<0.001 ***
			<0.01 **
			<0.05*
DW	5.21	440.00	***
DA	8.16	214.60	***
DAY	7.77	125.60	***

1 Table 2: Output of a GAM fitted to the daily locations of newborn grey seal pups at
 2 the study site on the Isle of May during the 2000 breeding season (a) with
 3 predicted aggression included as a variable, (b) without predicted aggression.
 4 DW = Distance to water, DA = Distance to access, NP = Neighbouring pups,
 5 AGG = Aggression, Day = Day.

6

7 (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	***

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10 (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	***

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1 Table 3: Akaike Information Criteria (AIC) values for the likelihood of observed grey
2 seal pup distributions occurring under the simulation models with and without
3 aggression and the null model on surveys 2, 3 and 4. Values shown represent
4 likelihoods derived when the upper- and lower-most replacement probabilities were
5 incorporated. Lower AIC values indicate a better model fit.

6

	Upper replacement probability			Lower replacement probability		
	Simulation with aggression	Simulation without aggression	Null	Simulation with aggression	Simulation without aggression	Null
Survey 2	712.75	691.29	654.30	712.70	691.24	654.29
Survey 3	676.65	664.94	624.29	791.10	664.88	624.28
Survey 4	346.93	355.98	281.18	575.85	813.88	281.16

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1 **Figure Legends**

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

9

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

12

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

16

17 Figure 4: The (a) observed, (b) simulated with aggression, (c) simulated without
18 aggression and (d) null grey seal pup distributions on surveys 2, 3 and 4. The
19 legend only corresponds to the simulated and null distributions. In the
20 observed distributions, black = 0 pups, grey = 1 pup, white = 2 pups.

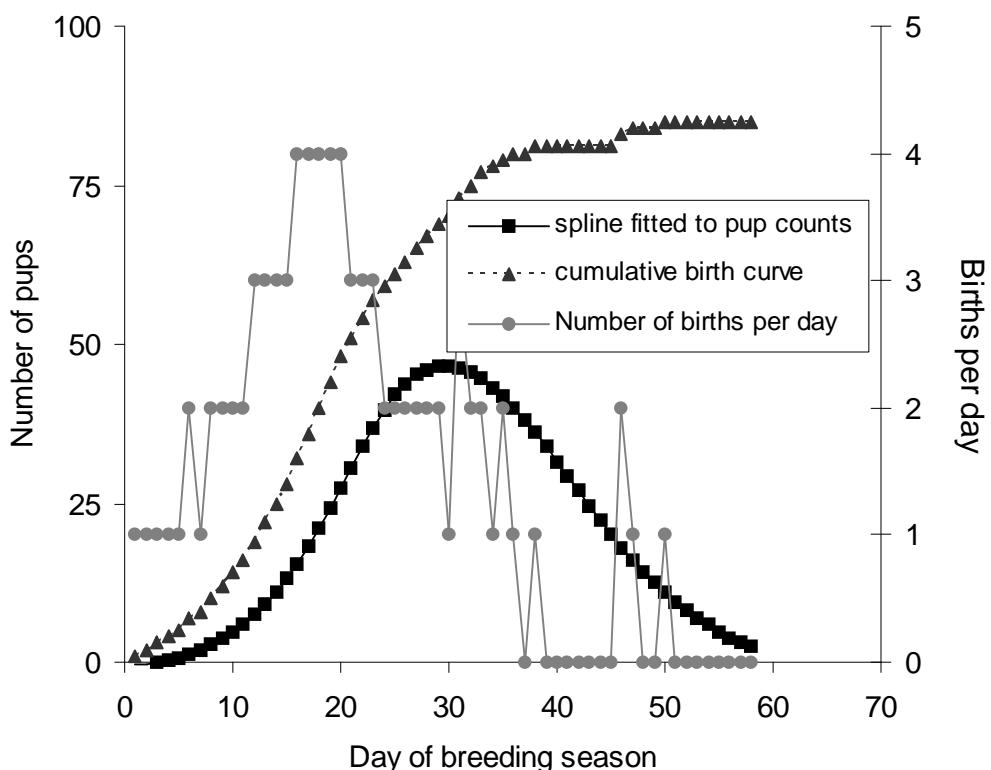
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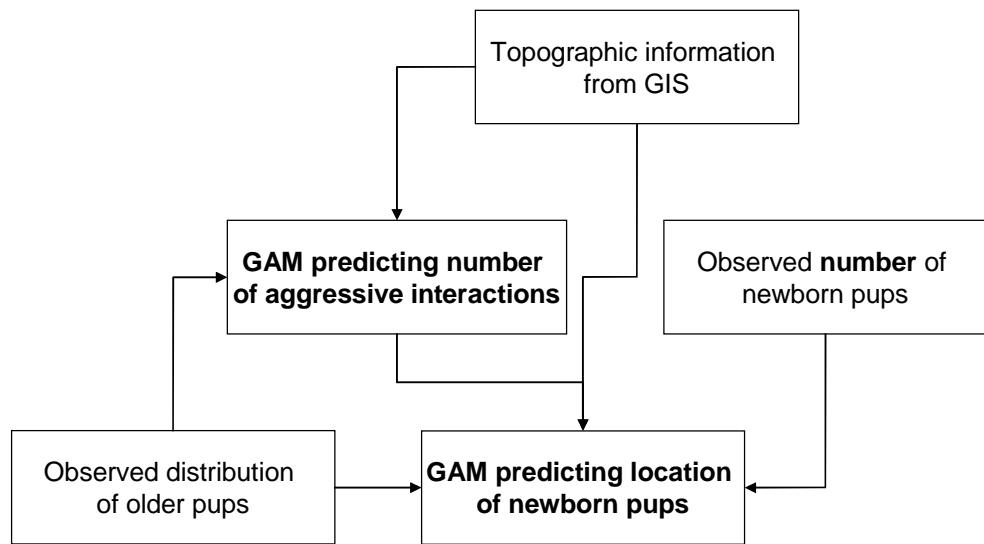
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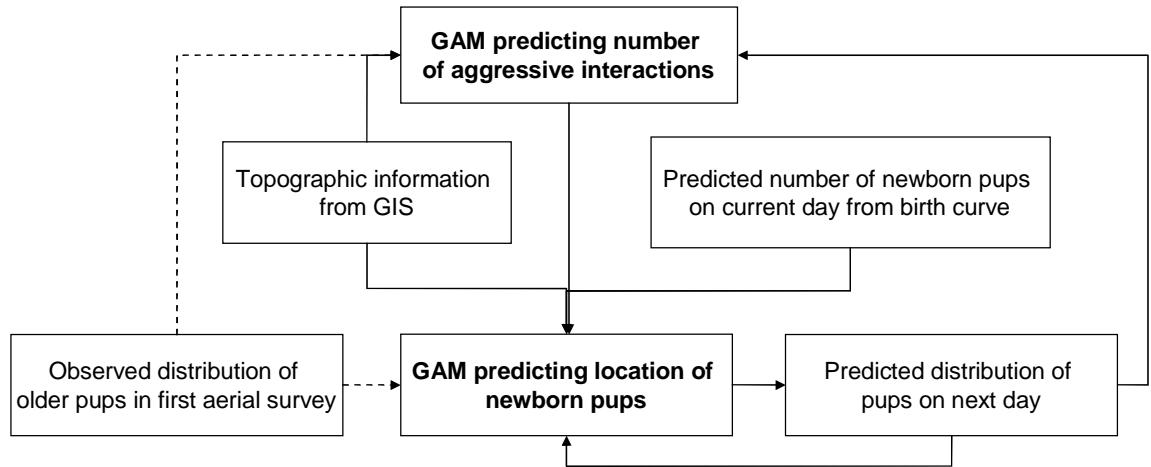
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