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**Factors affecting the distribution and abundance of grey
seals (*Halichoerus grypus*) around the UK.**

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A thesis submitted to the University of St. Andrews for the degree of Doctor of
Philosophy.

Division of Environmental and Evolutionary Biology

13 January 2003



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Declarations

I, Catriona M. Stephenson, hereby certify that this thesis, which is approximately 33,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

Date 28/4/03

Signature of Candidate

I was admitted as a research candidate in October 1999 and as a candidate for the degree of Philosophy in October 2000; the higher study for which this is a record was carried out in the University of St. Andrews between 1999 and 2002.

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I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of philosophy in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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Abstract

The UK grey seal (*Halichoerus grypus*) population has been increasing steadily for at least 30 years. During this period, the number of pups born at all major colonies has been monitored annually by the Natural Environment Research Council (NERC) Sea Mammal Research Unit (SMRU) using aerial photography. Some colonies have remained constant for decades, many have increased exponentially, and a few have decreased or even become extinct. The aim of this study was to identify the environmental factors that determine where a female grey seal chooses to give birth, in order to develop predictive models of colony spread.

A technique for extracting fine resolution data on topography and seal distribution from aerial survey photographs was developed and applied to a number of colonies in Orkney, Scotland, in different years. There was a consistent relationship between pup location and distance to water and slope at these colonies, but a varying relationship between pup location and distance to access to the sea.

The occurrence of aggression between female seals at the Isle of May in the 2000 breeding season could be predicted using models fitted to observations of variables that are measurable in aerial photographs. The locations of newborn pups could be modelled by a combination of topography, and variation in the presence of conspecifics and aggressive behaviour over time. These models were used to simulate variations in levels of aggression and hence pup distributions in space and time on two colonies in Orkney. The general applicability of the Isle of May models was limited, probably due to a number of specific characteristics of the original study site. However, the model did identify areas of preferred habitat towards the middle and end of the breeding season when the numbers of pups on an island is greatest.

Chapter 1

General Introduction

1.1 General Introduction

1.1.1 Population biology of the grey seal in the UK:

The order Pinnipedia includes all the seals, sea lions, fur seals and walruses. It is made up of two superfamilies: the Otarioidea and the Phocoidea. The Otarioids consist of the eared seals (family Otariidae) and the walruses (family Odobenidae) and the Phocoids contain the true seals (family Phocidae). There are 18 phocid species found throughout the world today and these are divided into two subfamilies the Monachinae and the Phocinae. The Monachines are predominantly found in southern regions and consist of the two species of tropical monk seals, the four species of Antarctic seals, and the two species of elephant seals. There are 10 species of Phocinae and all are found in the Northern Hemisphere. The grey seal, *Halichoerus grypus* (Fabricius, 1791) (Figure 1.1) is one of the largest of the Phocinae and is restricted to the western and eastern North Atlantic Ocean (extending into the Barents Sea) and the Baltic Sea (Bonner and Thompson, 1981) (Figure 1.2). Forty percent of the world's population breeds around the UK and 92% of the UK population breeds in Scottish waters (Figure 1.3).

In the UK, grey seals breed between the months of August and December, although locally the breeding season only lasts for 1-2 months. Breeding is colonial, usually on uninhabited offshore islands. Within a colony, females aggregate when they come ashore. Once a suitable pupping site has been found, a female gives birth to a single white-coated pup. She stays with the pup for a lactation period of 17-20 days. During this time, females are often seen moving to and from the sea, but they appear to feed very



(a)



(b)



(c)



(d)



(e)



(f)



(g)

Figure 1.1: Grey seal (a) female, (b) male and (c-g) pups representing each of the five developmental stages.

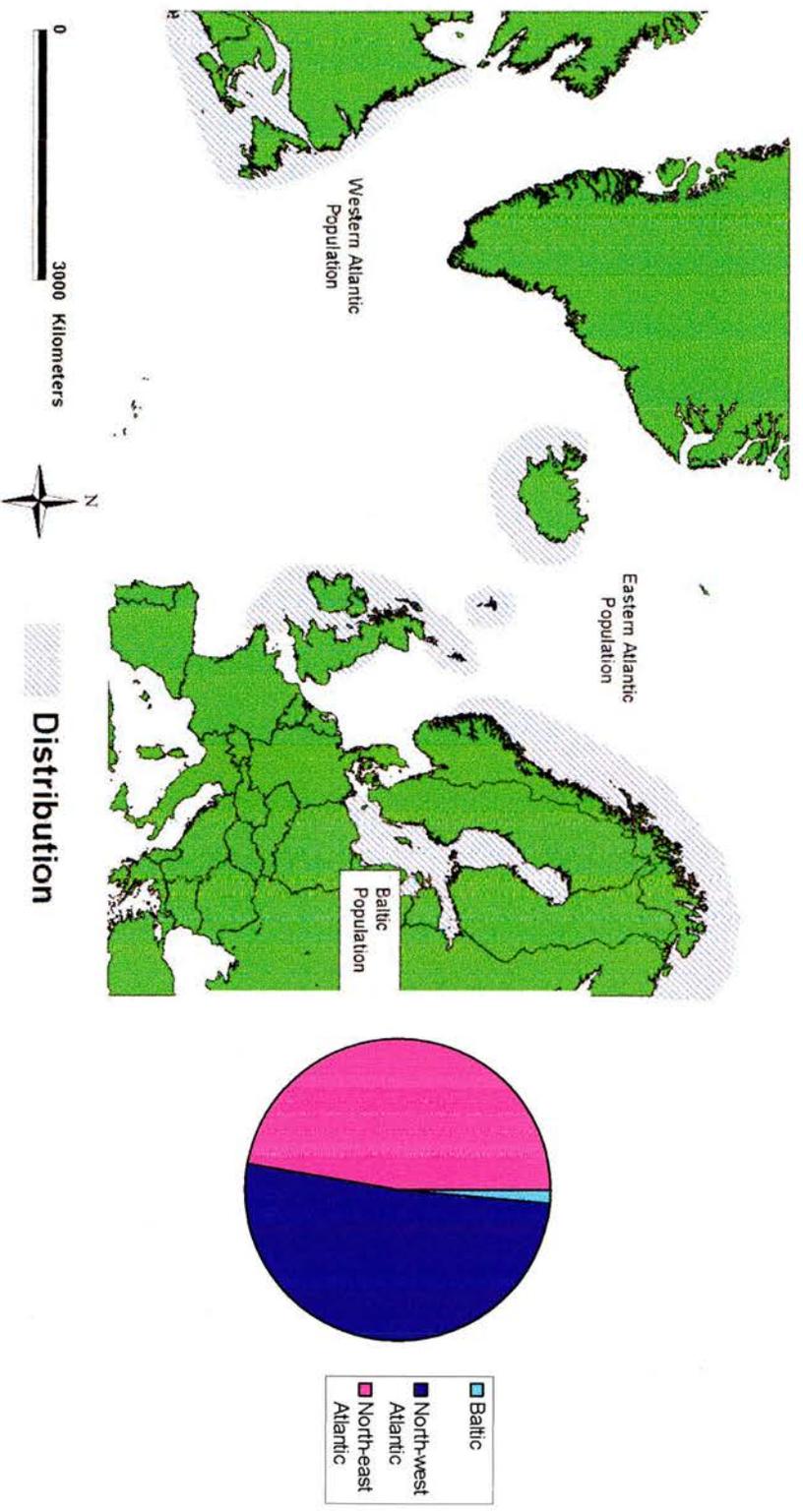


Figure 1.2: The distributions of the 3 main populations of grey seals and the proportion of the total world population found in each.

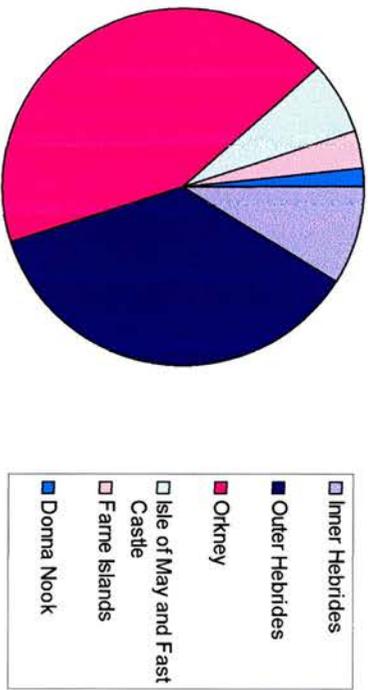
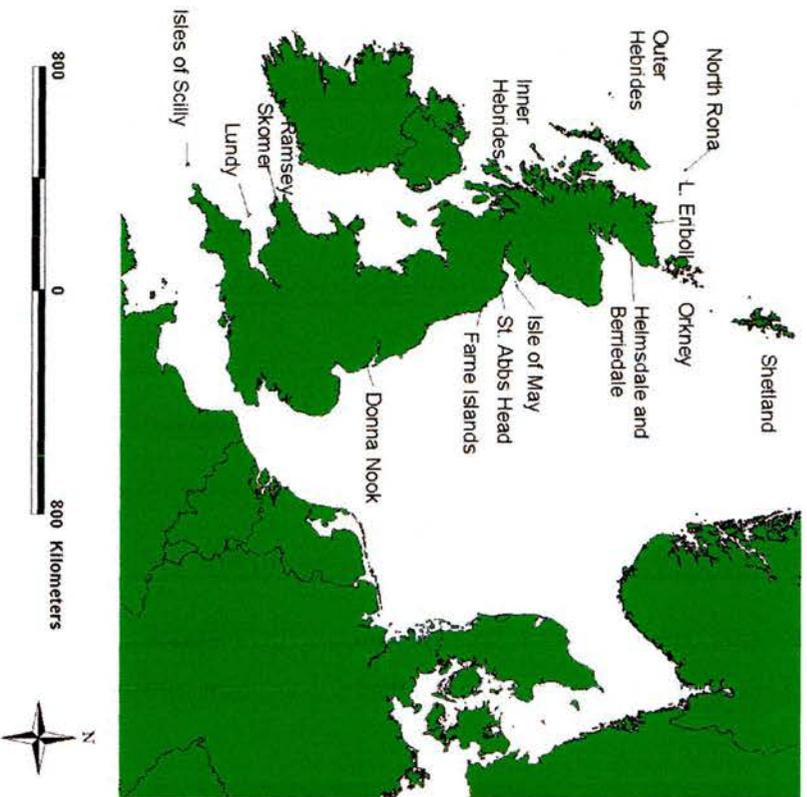


Figure 1.3: The main grey seal breeding colonies around the UK and the proportion of the total UK population found in each.

little, if at all, and rely on their blubber stores for maintenance and milk production (Fedak and Anderson, 1982). Two or three days prior to weaning their pups, females come into oestrus and are usually mated before they leave the colony. Around the time of weaning the pup sheds its white coat, known as the lanugo, and undertakes a postweaning fast on land for between 10 and 28 days (Reilly, 1991; Hall, 2002). The development of a pup during its time on the breeding patch has been divided into five stages (Boyd *et al.*, 1962), stages 1 to 3 have white natal coats, during stage 4 pups start to moult and by stage 5 they are fully moulted and generally weaned (Figure 1.1). Sexual maturity occurs at four or five years of age in females and six to eight years of age in males. Adult females are pregnant year round as the gestation period lasts 12 months, although this includes a delayed implantation period of four months.

The UK grey seal population has been increasing at between 5-6% annually for at least the last four decades. In 2001 the total population was estimated to be around 144,500 individuals (Special Committee on Seals (SCOS), 2002). However, since 1992 the annual rate of increase in pup production has decreased from 5.2% between 1992 and 1996 to 2.8% between 1997 and 2001 (Table 1.1). The continuing increase in population size has been a result of both protective legislation and a decline in the size of island communities around Scotland, which has increased the area of land available for breeding (Hiby and Duck, in press; Summers, 1978).

Table 1.1: Pup production, total population estimates for 2001 and annual changes in pup production over 5 year periods for annually monitored sites, and pup production and total population estimates for sites that are only monitored occasionally (SCOS, 2002).

Location	2001 pup production	Annual change in pup production			Total 2001 population (to nearest 100)
		1987-1991	1992-1996	1997-2001	
Inner Hebrides	2,938	+4.2%	+2.5%	-0.5%	10,600
Outer Hebrides	12,325	+5.1%	+2.2%	+1.4%	43,900
Orkney	17,523	+7.4%	+9.6%	+4.4%	58,300
Isle of May & Fastcastle	2,253	+14.0%	+3.9%	+3.3%	7,700
Farne Islands	1,247	+2.1%	+1.7%	-1.7%	4,300
Donna Nook	634	+39%	+14.6%	+14.5%	2,200
Subtotal*	36,920	+6.2%	+5.2%	+2.8%	127,000
SW England & Wales	1,500				5,200
All other sites	3,500				12,300
Total	41,920				144,500

- Subtotals calculated from annually monitored sites only.

1.1.2 Legal status of UK grey seals and conflicts with fisheries:

The grey seal was the first British mammal to be protected by law. In 1914 the Grey Seal Protection Act was passed because it was believed that the population had been reduced to 500 animals (Harwood, 1984), although this was probably a considerable underestimate. The 1914 Act was replaced by the Grey Seal Protection Act 1932, which protected pups during the breeding season and allowed the possibility of a future temporary withdrawal of protection should it be required. In the late 1950's a Consultative Committee on Grey Seals and Fisheries was established because the continuing rapid increase in seal numbers was causing conflict with the fisheries industry. Complaints from fishermen, and salmon fishermen in particular, led the Committee to recommend in 1963 that the grey seal stocks in Orkney and the Farne Islands should be reduced to three-quarters of their then current size by killing moulted pups during the breeding season (Harwood and Greenwood, 1985). Although some culling was carried out, both populations continued to increase (Summers, 1978). Currently, legislation is based on the Conservation of Seals Act 1970. In 1977 a new management plan was devised to reduce the grey seal population of the Outer Hebrides and Orkney from 50,000 to 35,000 by the end of 1982. In order to achieve this, 5,400 cows and 24,000 pups were to be killed on breeding beaches over a five year period (Summers and Harwood, 1979). Due to problems of logistics, the target numbers were not reached in 1977, but the indirect consequences of the cull probably resulted in a greater reduction in numbers than was initially anticipated. In particular, the presence of hunters in a colony probably reduced pup survival and adult fecundity as a result of desertion, pupping in unsuitable places, and poor fertilisation rates (Summers and Harwood, 1978). The culling

programme was abandoned in 1978 as a result of public opposition (Harwood and Greenwood, 1985). Conservation bodies were concerned that although grey seals are common in the UK their world population is relatively small. They argued that a more detailed justification for the cull was required, that accounted for uncertainties involved in the calculation of seal numbers, diet and daily food requirement (Harwood and Greenwood, 1985).

Aerial surveys of all the major grey seal breeding colonies around the UK commenced in 1963 and have been conducted annually ever since (Duck *et al.*, submitted) by the Sea Mammal Research Unit (SMRU). This time series of surveys allows SMRU to provide estimates of the UK seal population size so that the Natural Environmental Research Council can fulfil its obligation under the Conservation of Seals Act, 1970 and related Orders to provide advice to the Department of Environment, Food, and Rural Affairs (DEFRA), and the Scottish Executive (SE) on the management of seals (Harwood, 1997). As well as being protected within the UK, the grey seal is listed as a “Species of Community Interest” under the European Council Directive 92/43/EEC (“The Habitats Directive”). One of the aims of this Directive is to ensure the favourable conservation status of 632 species of animal and plant by establishing and monitoring a network of Special Areas of Conservation (SACs). The long time-series of grey seal aerial surveys has provided much of the information necessary to identify candidate SACs within the UK for this species.

The initial driving force for the population monitoring programme was the perceived conflict between seals and fisheries. There is an increasing amount of evidence that suggests that grey seals and fishermen do not always compete for the same fish (Hammond *et al.*, 1994; McConnell *et al.*, 1984). However, as fish stocks continue to decline there is potential for increasing conflict. New methods are being developed to estimate diet and how this is related to prey availability and to determine where seals forage (Fedak, 1996). This information will make it possible to determine the nature of the competition between seals and the fishing industry. Hammond and Harwood (1985) estimated that grey seals in the North Sea consumed 57,000 tonnes of fish per year, based on diet samples collected in 1984 and 1985. Most of this consumption was sandeels (61%) and cod (19%) (Harwood and Croxall, 1988). The relative importance of seal predation can be evaluated by comparing seal consumption to fisheries catch (Beverton, 1985). The consumption of commercially important fish species in the North Sea in the mid-1980's was one or two orders of magnitude lower than the amount removed by the fisheries, with the exception of sandeels (Harwood and Croxall, 1988). However, the grey seal population has doubled since the mid-1980s and the cod quota has been severely cut. If the seals' diet has not changed since the mid-1980s, the seals could be consuming an amount of cod equal to approximately half of the UK cod quota. A new study is now underway to determine the current diet of seals in the North Sea and elsewhere around the UK.

1.1.3 Monitoring current trends and predicting future trends:

Conducting surveys to estimate the population size of marine mammals is difficult because they spend a large proportion of their time underwater (Hammond, 1995). Grey seals spend over 80% of their time at sea (McConnell *et al.*, 1999), and 85-90% of this time underwater (Thompson, 1991). The SMRU aerial survey takes advantage of the fact that grey seals have to spend a proportion of their time on land (or ice) during the breeding season (Hammond, 1995). Even at this time, only breeding animals are available for counting, and the survey results can only be used to estimate the number of pups born each year (Thompson *et al.*, 1988). Additional information, such as fecundity and survival rates, must be used to convert the estimate of the number of pups born to an estimate of total population size (Hiby and Harwood, 1985).

A series of aerial surveys are carried out over the course of the breeding season because the spread of pupping dates at each colony exceeds the length of stay of individual pups. As a result, no individual survey will include all the pups born (Harwood, 1997; Ward, 1987). Stochastic modelling of the pupping process and the development of the pups through the breeding season, along with the data from the aerial surveys, has generated a 40 year time series of pup production estimates for the majority of the UK colonies (Duck *et al.*, submitted). Many other studies, including ground counts and ground-truthing have helped to make the estimates of pup production as accurate as possible (eg. Wyile and Thompson, 1985).

Clearly the UK grey seal population cannot continue to grow at a rate of 5-6% per year indefinitely. Most organisms show some evidence of density-regulating mechanisms that slow the growth rate when a threshold density is exceeded. Density-dependent changes in fecundity and juvenile survival have been demonstrated in pinniped populations (Harwood and Rohani, 1996). However, the only density-dependent relationship that has been described so far for grey seals involves the survival of pups from birth to weaning (Bonner, 1975; Coulson and Hickling, 1964; Harwood and Prime, 1978). The decrease in survival appears to be caused by a disproportionate increase in the number of deaths due to desertion and injury at high densities within a breeding colony (Coulson and Hickling, 1964). Fogden (1971) showed that the mother-pup bond can be broken by disturbance in congested assemblies. However, this density-dependence relationship has a very weak effect on population growth rate (Harwood, 1981) and is insufficient to limit population numbers. Adult survival is a much stronger regulator of population growth than pup survival, and density-dependence in this parameter is more likely to generate a stable population (Harwood and Rohani, 1996). Although it is unlikely that pup survival will ever decline to the level necessary to stabilise the population, the effects of high density may extend into the post-weaning period and survival during the first year of life could be reduced to the necessary level (Harwood, 1981).

In order to understand more about population regulation we need to identify the factors that may be important in determining population size and understand how these factors operate. Both extrinsic and intrinsic factors may be important (Nicholson, 1957) but

Caughley and Krebs (1983) concluded that extrinsic factors are likely to be more important in large mammals, such as marine mammals. Pinnipeds have few natural enemies, particularly the grey seal around the UK, and predation is unlikely to affect population dynamics. Although disease might be a problem, in marine mammals it generally causes density-independent mortality (Harwood and Hall, 1990). Two other extrinsic factors likely to be involved in population limitation are food availability and space. The increase in seal numbers and intensive fishing may have changed the structure of prey communities, perhaps reducing some of the preferred prey of seals to low levels. Grey seals feed on a wide variety of fish (Hammond *et al.*, 1994) and such generalist predators are thought to be able to switch to alternative prey species when their preferred prey declines in number (Fryxell and Lundberg, 1994; Furness, 1996). However, prey switching has been shown to have an adverse effect on the body condition of common seals in Scotland (Thompson *et al.*, 1997), which may have a subsequent effect on fecundity. Other examples of changes in seal fecundity related to food availability have usually been linked with an episodic collapse in a local prey populations rather than seal population density (Harwood and Rohani, 1996).

In terms of space availability, the physical features of a space can be just as important as the biological features (Harwood and Rohani, 1996). For the grey seal, the most important feature of space is likely to be the availability of suitable areas for breeding. Space during the breeding season may be a limiting factor because grey seal females become intolerant of conspecifics once they have given birth (eg. Boness *et al.*, 1982; Harcourt, 1990; Pomeroy *et al.*, 2000a). This intolerance often leads to aggressive

encounters between individuals that may serve as a pup protection mechanism (Boness *et al.*, 1982). Such an interaction, where one individual prevents another from exploiting a resource is referred to as “interference”. In these circumstances aggressive behaviour acts as a density-regulating mechanism. Caudron (1998) found that grey seal females approaching conspecifics with pups on the Isle of May were threatened if they were closer than two body lengths. The median nearest neighbour distance between adult females in this colony was 2.3-3.4m, which corresponds to a local animal density of approximately one adult per 10m². Any increase in local density above this level could affect both pup and adult survival (Harwood, 1976).

At the moment there appears to be an abundance of suitable breeding habitat for grey seals around the UK, provided that animals can disperse to new breeding sites. There are two general forms of dispersal: natal dispersal, which is the movement between the birthplace and the first breeding place; and breeding dispersal, which is the movement between successive breeding attempts (eg. Greenwood, 1980; Greenwood and Harvey, 1982). Dispersal in grey seals appears to be predominantly natal, because adults appear to show a high degree of site fidelity (Amos, 1995; Pomeroy *et al.*, 1994). First-time breeders appear to return to the site at which they were born (Pomeroy *et al.*, 2000b), but they may not be able to compete successfully for space because of their smaller size and inexperience. Harwood and Gaggiotti (1999) suggested that grey seals show fitness-related dispersal, as proposed by Ruxton and Rohani (1999). They hypothesised that grey seal pups will return to their natal colony when they breed for the first time (and all subsequent times) unless their likely fitness at this site is below some threshold value; if

their anticipated fitness is below this threshold, then individuals will seek out sites at which their fitness is higher. We can only speculate on what will happen when all suitable patches are occupied up to the threshold for fitness-related migration. At this point, fitness will be identical in all patches and animals breeding for the first time will have the choice of not breeding at all (and therefore gaining zero fitness), or accepting a fitness level below their current threshold.

If we are to discover how the number of habitable breeding sites limits long-term grey seal abundance, we need to be able to identify all habitable sites that are currently vacant (Begon *et al.*, 1996). Understanding the ecological requirements of a species can help predict the effects of future habitat changes, define areas for species protection or reintroductions (eg Macdonald *et al.*, 2000) and identify areas where human-wildlife conflicts may occur (Arthur *et al.*, 1996; Hirzel *et al.*, 2001). Through the aerial surveys and ground counts, there is good information on the sites currently used by grey seals for breeding but very little is known about what makes these sites suitable. Defining a suitable site is problematic both theoretically and empirically (Begon *et al.*, 1996). Most unoccupied areas in the world are unsuitable for most species, either through natural causes or human activities, but there are also areas which are intrinsically suitable but which are, as yet, unoccupied (Thomas and Kunin, 1999). Only rarely has the identification of suitable but unoccupied sites been attempted. One possible method involves identifying the characteristics of occupied sites and then determining the distribution and abundance of similar sites to determine boundaries of spread (Begon *et al.*, 1996).

1.1.4 Factors that may affect the choice of suitable pupping sites:

When a female grey seal is looking for a suitable pupping site many factors may be involved in her choice. Females are the first animals to come ashore in the breeding season so they are the initiators of the colonisation process. Individual females may investigate potential sites on several occasions over a period of up to three weeks before they actually give birth (Burton *et al.*, 1975). Disturbance during these investigations may cause the female to look elsewhere for a suitable site. Sites close to an access point to the sea or an inland pool appear to be more attractive than those that are a long way from water (Anderson *et al.*, 1975; Pomeroy *et al.*, 1994; Redman *et al.*, 2001; Twiss *et al.*, 2000a). For example, on North Rona females aggregate around the access gullies (Pomeroy *et al.*, 1994) and the few pools that are present at the start of the season (Anderson *et al.*, 1975). As the area of waterlogged ground increases during the season, the animals become more widely spaced as more sites close to water become available (Redman *et al.*, 2001). The choice of sites close to water may be related to the problem seals face in keeping cool whilst on land, as keeping the body wet may assist in controlling body temperature (Anderson *et al.*, 1975; Twiss *et al.*, 2002). Twiss *et al.* (2000a) classified sites close to water as “low cost”, because of the relatively short distance individuals had to travel to get to water. However, breeding at these sites may incur additional costs such as increased pup injuries and mortality, and increased time spent on aggression towards other females (Twiss *et al.*, 2000a). Caudron (1995) also showed that higher densities of pups occurred where the substrate was pebbles, gravel or sand than on rocky substrates. High densities of pups are also found on vegetated areas

and where drainage ditches or natural water courses provide access routes to the sea or freshwater pools (Caudron, 1995).

Most of the published studies of grey seal habitat preferences have been qualitative rather than quantitative and, in the UK, they have focussed on two breeding colonies, the Isle of May and North Rona. Twiss *et al.* (2001) quantified fine scale habitat use in relation to topographical parameters at two locations on the Isle of May, but they only considered the average distribution of pups over a single breeding season. However, the environment provided by a grey seal colony changes constantly over the breeding season as a result of changing weather conditions, changing availability of inland pools of water and the arrival and departure of conspecifics. Therefore the conditions for pupping perceived by a newly arrived female will change at least on a daily basis.

The grey seal breeding season lasts 7-8 weeks, but each individual female only remains on the colony for 18-20 days. This means that there is a turnover of occupancy during the pupping season. As a result previously occupied pupping sites become available for colonisation by later-arriving females. Therefore, we can identify areas of suitable habitat and predict the spread of animals across a landscape by investigating the way in which animals distribute themselves both within and between breeding seasons. The aerial photographs taken annually by SMRU allow both temporal scales to be examined, because four or five surveys are carried out each season.

1.1.5 Use of remotely-sensed data, GIS technology and spatio-temporal modelling for assessing habitat preference:

Remote-sensing, geographical information systems and spatio-temporal modelling have become increasingly useful tools for identifying suitable habitat and predicting the spread of wildlife. Remote-sensing is a collective term used for techniques that gather information about an object from measurements made at a distance. Remotely-sensed data are being used increasingly by biologists to learn more about the interactions between species and their environment on a variety of scales. Many birds and mammals have been tracked using satellite telemetry, in order to understand their migrations (eg. red-crowned cranes, *Grus japonensis* (Higuchi *et al.*, 1998), elephants, *Loxodonta africana* (Verlinden and Gavor, 1998), green turtles, *Chelonia mydas* (Luschi *et al.*, 1996), humpback whales, *Megaptera novaeangliae* (Mate *et al.*, 1998)) and foraging patterns (eg. Humbolt penguins, *Spheniscus humboldti* (Culik and Luna-Jorquera, 1997), grey seals, *Halichoerus grypus* (McConnell *et al.*, 1992b; McConnell *et al.*, 1999), southern elephant seals, *Mirounga leonina* (McConnell *et al.*, 1992a)). Aerial surveys provide more static views of species distributions and are particularly useful for estimating abundance, particularly when the animals are known to be aggregated (eg. grey seal pups, *Halichoerus grypus* (Duck *et al.*, submitted; Hiby *et al.*, 1988), Steller sea lion pups, *Eumetopias jubatus* (Snyder *et al.*, 2001), walrus, *Odobenus rosmarus* (Barber *et al.*, 1991), northern elephant seals, *Mirounga angustirostris* (Lowry *et al.*, 1996) and manatees, *Trichechus manatus latirostris* (Wright *et al.*, 2002)).

On their own, these remote-sensing techniques can help us to understand more about a species behaviour and activity patterns, but in conjunction with habitat data the underlying reasons for the observed behaviours can be inferred. Habitat types and their distributions are often obtained from ground based surveys of areas of interest but remote-sensing techniques can provide us with longer term, more continuous data over larger scales (Roughgarden *et al.*, 1991). Useful spatial parameters can be extracted from satellite and aerial imagery on a number of temporal and spatial scales, for example, classification of vegetation types such as forestry (Fox *et al.*, 2000; Franklin *et al.*, 2000), land and ocean surface temperatures, chlorophyll a concentrations from ocean colour indices (Roughgarden *et al.*, 1991), and elevation from stereo aerial images (eg. Perry *et al.*, 1999). Observed species distributions can then be related to appropriate aspects of the surrounding environment in order to increase our understanding of a species' ecology and to identify which habitat types are important for its persistence.

Geographical Information Systems (GIS) are computer systems that allow the storage and visualisation of layers of spatial data. They have been used extensively to assess relationships between species and habitat (eg. Bian and West, 1997; Debinski *et al.*, 1999; Kurki *et al.*, 1998; Strager *et al.*, 2000), to investigate the effects of changing environmental conditions (eg. Walker, 1990; Wright *et al.*, 2002), and to evaluate management options (eg. Macdonald *et al.*, 2000). Many GIS packages have limited analytical capabilities (Guisan and Zimmermann, 2000) but they can be powerful analytical tools if they are combined with statistical packages.

The ability to predict species distribution is an important element of conservation and management (Hirzel *et al.*, 2001). Multivariate models are often used to define habitat suitability for a given species or community of species (Guisan and Zimmermann, 2000). Generalised linear models (GLMs) are generalised versions of multiple regression analysis and have often been used to model the spatial distributions of species from gridded survey data and spatial variables (Augustin *et al.*, 1996). GLMs allow flexible models to be constructed using statistical distributions other than the Normal distribution, for example count data (Poisson distribution) or presence/absence data (Binomial distribution).

The predictive ability of a species distribution model is one of its most valuable uses. It is important that the model fits well to the observed data but it is also important that it can be used to predict distribution in those parts of the species' range where less detailed information is available. The grey seal colonies at the Isle of May and North Rona (Figure 1.2) have been intensively studied for a number of years and there are a number of qualitative descriptions of the factors that appear to be influential in a females decision of where to pup (Anderson and Harwood, 1985; Boyd *et al.*, 1962; Pomeroy *et al.*, 1994; Pomeroy *et al.*, 2000a; Prime, 1981; Prime, 1982). However, few ground-based studies have been carried out elsewhere in the UK, and it is unclear whether the factors identified at the Isle of May and North Rona are universally important. The grey seal breeding colonies in Orkney (Figure 1.2) are ideal sites at which to study grey seal patch expansion and development because they have shown the biggest increase in pup production in recent years and the number of colonies has increased from 15 in 1960 to 21 at present.

In contrast, pup production in the Hebrides has been relatively constant since 1992 and these colonies may have been a source of immigration into Orkney in recent years. The aerial survey photographs of the Orkney breeding colonies can be used to document a detailed history of the spread of seals within and between breeding seasons. These data provide an independent data set with which to test the predictive ability of habitat suitability models derived from intensively-studied colonies. If such models are able to predict the changes in seal distribution observed in Orkney then they may also be able to predict the extent to which existing colonies will continue to expand and where new colonies are most likely to be established.

1.2 Outline and Aims of the Study

The overall aims of this study were to identify the environmental factors that determine where a female grey seal chooses to give birth to her pup to develop predictive models of how far existing colonies will spread.

Chapter 2 describes the development of computer simulations that were used to predict the distribution of pups on an island under a range of hypotheses about the processes that may determine where a female grey seal gives birth. These simulations were then used to assess the potential power of data extracted from aerial photographs to distinguish between these hypotheses.

In Chapter 3, I describe the development of techniques to generate topographical surfaces of grey seal colonies and detailed maps of pup distributions using data extracted from photographic images. Until now the aerial photographs of grey seal breeding colonies had only been used to obtain counts of pups. The availability of high-resolution scanners, GIS technology and substantial disk space opened up opportunities for extracting additional data from these photographs. Photographs were digitised, rectified and tessellated to eliminate overlap. As the data were not collected for this purpose, techniques that took account of problems associated with the data set, such as limited overlap and lack of fiducial marks, had to be developed. Repeat counts of the original photographs and the digitised images were carried out by experienced and inexperienced counters to determine the accuracy of the technique.

In Chapter 4, I use data extracted from aerial photographs to determine whether the relationships between grey seal breeding distribution and habitat characteristics identified from detailed studies at the Isle of May and North Rona also apply to three breeding colonies in Orkney.

Chapter 5 describes the results of detailed behavioural studies conducted at the Isle of May to determine whether a female's decision of where to pup is affected by the amount of aggression that she is likely to encounter in a given habitat as well as by the site's topography. Aggressive encounters occur predominantly between females defending their pups, so aggression may regulate the density of females that will give birth in an area. The aims of the observational study were to determine if the occurrence of

aggression could be modelled using variables that are measurable from the aerial photographs and if the locations of newborn pups could be predicted by a combination of topography, presence of conspecifics and aggressive behaviour over time and space. GLMs were used to model both the occurrence of aggression encounters and newborn pups.

In Chapter 6, the general applicability of the models developed for the Isle of May was tested by generating predictions of pup distribution over time for two breeding colonies in Orkney, which were then compared with distributions extracted from the aerial photographs.

Chapter 2

Simulations of an Idealised Grey Seal

Breeding Patch.

2.1 Introduction

The Sea Mammal Research Unit carries out annual aerial surveys of all the grey seal breeding colonies around Scotland to estimate pup production using high-resolution colour photographs (Hiby *et al.*, 1988). Until recently the photographs have only been used to provide counts of pups. However, detailed data on the actual distribution of pups can be extracted from these photographs, and these will increase our understanding of the ecological requirements of breeding grey seals (Caudron, 1995). Behavioural studies have implicated a number of topographical and behavioural factors that may be influential in determining the overall distribution of female grey seals and their pups on a breeding colony.

When a female grey seal comes ashore the physical and topographical features of a colony are likely to influence her selection of a pupping site (Pomeroy *et al.*, 1994; Pomeroy *et al.*, 2000a; Twiss *et al.*, 2000a). For example, an individual's position on a breeding colony appears to be influenced by the presence of water because the distribution of seals is often aggregated around access gullies to the sea and inland pools (Anderson *et al.*, 1975; Redman *et al.*, 2001; Twiss *et al.*, 2000a). It is thought that going into water may help with thermoregulation (Anderson *et al.*, 1975; Twiss *et al.*, 2002). Pupping sites close to water appear to be preferred, but the benefits gained by pupping at these preferred sites must be balanced against density-dependent costs, such as an increase chance of pup injury and mortality (Twiss *et al.*, 2000a).

Grey seals aggregate at breeding patches but, once they give birth, they become intolerant of approaching or nearby females, in order to protect their pups (Anderson *et al.*, 1975; Boness, 1982; Kovacs, 1987; Harcourt, 1990; Caudron, 1998). Caudron (1998) found that females who approached within two body lengths of another female with a pup tended to evoke an aggressive response. The median nearest neighbour distance she observed was 2.3-3.4m, which corresponds to a local animal density of approximately one adult per 10m². This implies that aggressive interactions may determine the maximum density of seals on a patch.

The aim of the study reported here was to use computer simulations to compare the predicted distribution of pups on an island under a range of hypotheses about the processes that may determine where a female seal gives birth with the distribution that would result from simple diffusion from an access point. Only factors that can be measured or estimated from the aerial photographs were included in these simulations. Simulations have been used widely in ecosystem management, for example, to test the applicability of overseas fire behaviour models to New Zealand ecosystems (Perry *et al.*, 1999) and to determine the factors leading to a lower aggregative response than expected in dark-bellied brent geese (Rowcliffe *et al.*, 1999).

Barriers to movement, including slope, the position of an access point to the sea, the position of water sources and aggression, as a density-regulating mechanism, are all

variables that may be extractable from the aerial photographs and influential in the movement patterns of grey seals across a colony.

2.2 Methods

Visual Basic for applications in Microsoft Excel, 97 (Jacobson, 1997) was used to simulate the arrival of seals at a discrete patch during the breeding season and also the factors involved in how they choose their pupping site. The basic model consisted of a patch 10 by 10 cells in size with an access point of four cells in the centre of the left hand side of the patch. Each cell was taken to represent 50m^2 , with a maximum density of five seals per cell. Thus, the patch represented 5000m^2 or half a hectare. The first move of each arriving seal could only be directly forwards or diagonally, its second move could only be forwards or sideways. Subsequent moves could be in any direction except directly backwards (Figure 2.2.1).

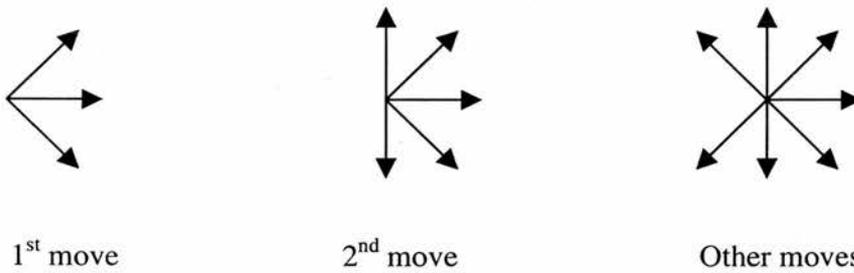


Figure 2.2.1: The possible directions that a seal can go depending on the move.

Each seal could only move by one cell at a time and the direction of each move was chosen randomly. The seal stayed in the first cell it entered that contained less than five seals. If a suitable cell was not found after 50 moves, the seal left the patch. With 150 seals arriving at the island, 50 moves per seal was sufficient to allow all

seals to find a space. In order to determine how many replicates of this programme were needed for the resulting distribution to be representative, the simulation was run 100, 200 and 300 times. There was no significant difference found between the three distributions (using a Pearson correlation matrix in SYSTAT 9, Figure 2.2.2), therefore 100 replications was considered sufficient in the remainder of the simulations.

Cost of locomotion:

It was assumed that the cost of locomotion to and from water was a linear function of the distance of a cell from the access point. The average distance from the access point to each cell by the shortest route was calculated. The programme was run as before but with the maximum permitted number of moves reduced to 40, 30, 20, 15, 10 or 5 moves. The average distance from access was plotted against the maximum number of steps allowed. For each simulation a histogram was also plotted showing the number of seals that moved 0-10m, >10-20m, >20-30m, >30-40m, >40-50m, >50-60m, >60-70m and >70-80m.

This was repeated with 300 and 500 arriving seals to determine if this affected the threshold number of moves required to find a space and the average distance moved.

Arriving and leaving:

For the following simulations 300 seals, each of which was allowed a maximum of 30 moves, were used. With this combination of parameters every seal found a

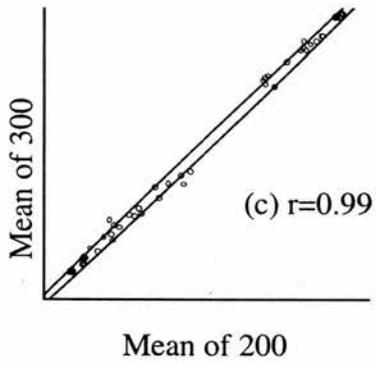
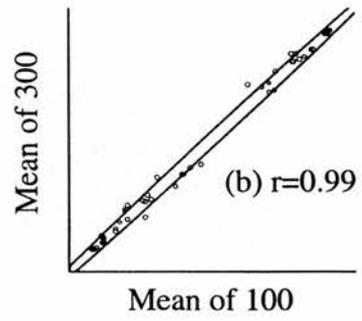
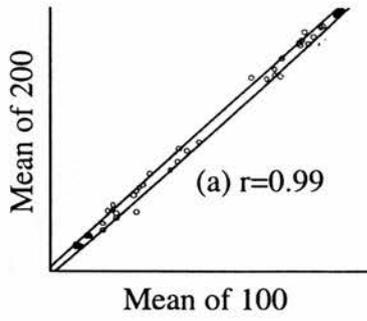


Figure 2.2.2: Pearson's correlations of the mean distance of occupied cells from access from (a) 100, (b) 200 and (c) 300 replicates of the null simulation.

suitable cell. Arrival of the 300 seals was staggered over the first 50 days of the breeding season in the following way:

4 per day on days 1 – 10

5 per day on days 11 - 20

8 per day on days 21 – 40

5 per day on days 41 – 50

This mimics the observed spread of births in an average grey seal breeding colony. Lactation in grey seals lasts for an average of 17 days (Hewer, 1960), at the end of which the female departs from the colony. To mimic this, the seals in the simulations were allowed to stay in their chosen cell for 20 days and then they left. As a result the number of seals present on the patch varied over the course of the breeding season (Figure 2.2.3).

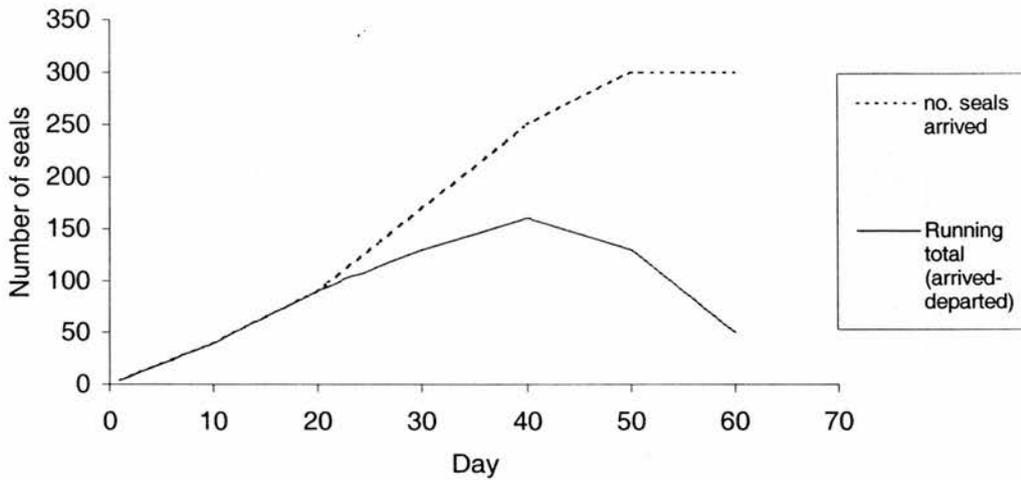


Figure 2.2.3: The number of seals that have arrived and the number of seals present on the patch over time.

The distribution was recorded on days 20 (after 90 seals arrived), 40 (250 seals arrived) and 50 (300 seals arrived). This mimicked the timing of the three aerial surveys that are usually conducted of each colony.

Influence of water:

A pool of water two cells in size was added to the patch in cells (5,7) and (6,7). The arriving seals could not choose areas within the pools as pupping sites. A null simulation was run with the pool present but without the seals being influenced by the presence of water. The average distance of each cell to water was calculated in the same way as the average distance to access. This allowed distance to access and water to be plotted against time. In a further set of simulations, the distance to water was used as part of a decision function by the arriving seals. When a seal entered a

cell, the distance of that cell to water was compared to that of all surrounding cells. If one of the surrounding cells was closer to water than its present location, then it was moved into that cell.

Density:

The potential effects of density were incorporated into the programme by combining the distance to water for a given cell with the present density in that cell using the following three functions:

Type 1: $F(\text{density}) = 1 - (0.1 * \text{density})$

Type 2: $F(\text{density}) = 1 - \exp(a * (\text{density} / 8 - 1))$ where $a = 5$

Type 3: if density < 1 then $F(\text{density}) = 1 - \exp(a * (b/8 - 1))$ else if density > 1 then $F(\text{density}) = 1 - \exp(a * (\text{density}/8 - 1))$ where $a = 5$ and $b = 4.5$

All three functions were multiplied by the distance to water of each cell and the resulting index determined whether a female stayed or moved on to another cell.

The Type 1 density function describes quality decreasing linearly as density increases (Figure 2.2.4). The Type 2 density function had little effect on the quality of a cell until the density in that cell was greater than or equal to four (Figure 2.2.4). This function allowed a maximum of five seals per cell in cells that were less than 20m from water. The Type 3 density function takes into account the gregarious nature of breeding grey seals (Figure 2.2.4). Empty cells or cells in which only one

other seal was present were considered to be of lower quality than cells with 2-4 other seals.

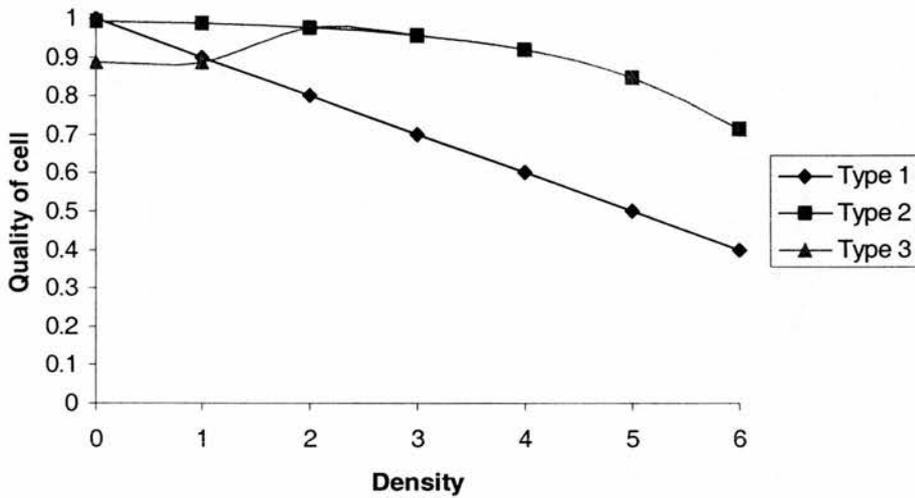


Figure 2.2.4: Relationship between density and the quality of a cell.

Differences from the null model:

100 replicates of each of the following models were run:

the null model,

water alone,

water plus density function Type 1,

water plus density function Type 2,

water plus density function Type 3.

To determine how distinct the predictions of the different models were from the null model, the 100 replicated distributions for each model were compared to 100 null distributions and the number of cells with matching seal densities recorded.

2.3 Results

Null model:

Figure 2.3.1 shows the mean distribution after 100 replicates of the null model. All cells close to the access point were fully occupied in each replicate.

Cost of locomotion:

The distance of each cell from the access point is shown in Figure 2.3.2. The proportion of available pupping sites occupied in each distance to access category when 150 seals arrived at the island is shown in Figure 2.3.3. The average distance from access was related to the maximum number of moves allowed (Figure 2.3.3a). No increase in the average distance from access was observed when the maximum number of moves for 150 seals was increased beyond 15. All pupping sites up to 30m from access were fully occupied when 150 seals were allowed to use the island and more than 10 moves were permitted (Figure 2.3.3b). When the number of seals arriving at the island was increased to 300 (Figure 2.3.4) the average distance moved plateaued at 40.5m after 15 moves. All pupping sites less than 30m from access were again fully occupied, but some seals spread as far as 70-80m from access (Figure 2.3.4b) if they were allowed 15 or more moves. Average distance travelled did not show a plateau when the number of seals arriving was 500 (Figure 2.3.5a). When 30 moves were allowed, nearly all pupping sites were fully occupied (Figure 2.3.5b). Even when only 10 moves were allowed, seals were still found up to 80m from the access point.

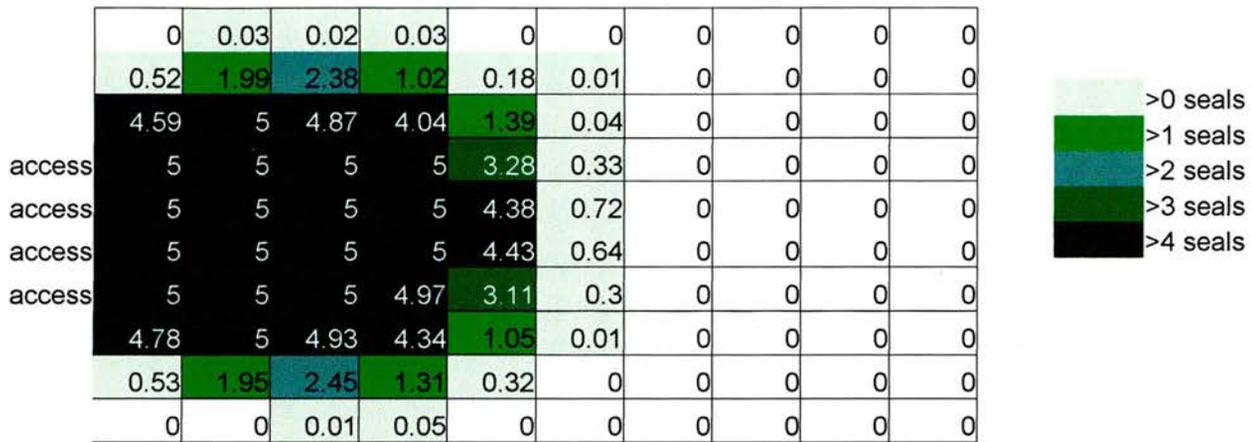
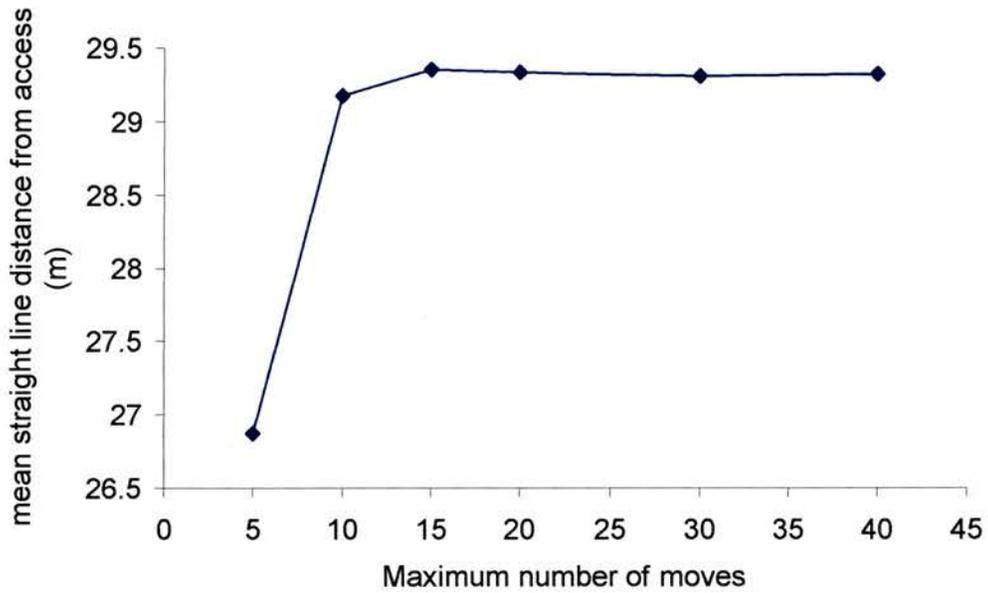


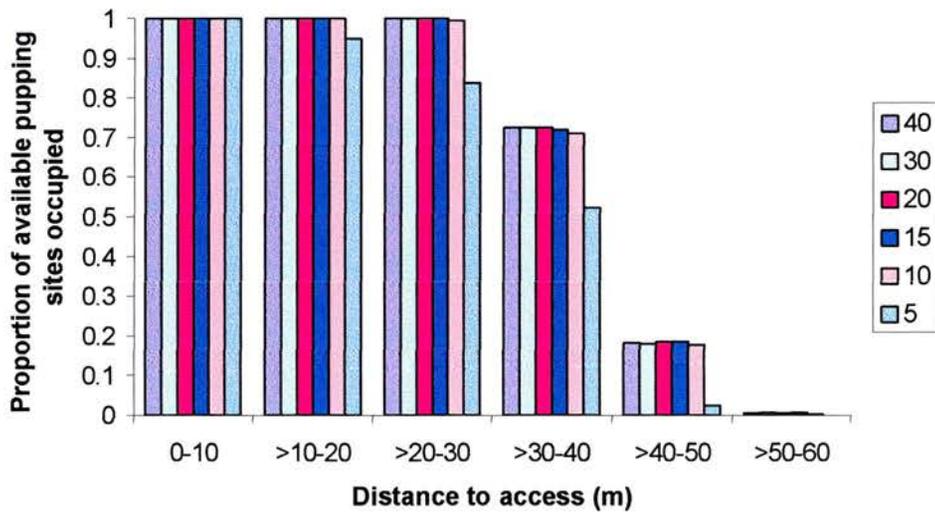
Figure 2.3.1: Mean representation of mean pup density after 100 replications of the null model.

	39.33	48.07	48.07	48.07	50.255	54.625	61.18	69.92	78.66	87.4
	30.59	39.33	39.33	41.515	45.885	52.44	61.18	69.92	78.66	87.4
	21.85	30.59	32.775	37.145	43.7	52.44	61.18	69.92	78.66	87.4
access	8.74	24.035	28.405	34.96	43.7	52.44	61.18	69.92	78.66	87.4
access	8.74	19.665	28.405	34.96	43.7	52.44	61.18	69.92	78.66	87.4
access	8.74	19.665	28.405	34.96	43.7	52.44	61.18	69.92	78.66	87.4
access	8.74	24.035	28.405	34.96	43.7	52.44	61.18	69.92	78.66	87.4
	21.85	30.59	32.775	37.145	43.7	52.44	61.18	69.92	78.66	87.4
	30.59	39.33	39.33	41.515	45.885	52.44	61.18	69.92	78.66	87.4
	39.33	48.07	48.07	48.07	50.255	54.625	61.18	69.92	78.66	87.4

Figure 2.3.2: The mean straight line distance in metres of each cell from access

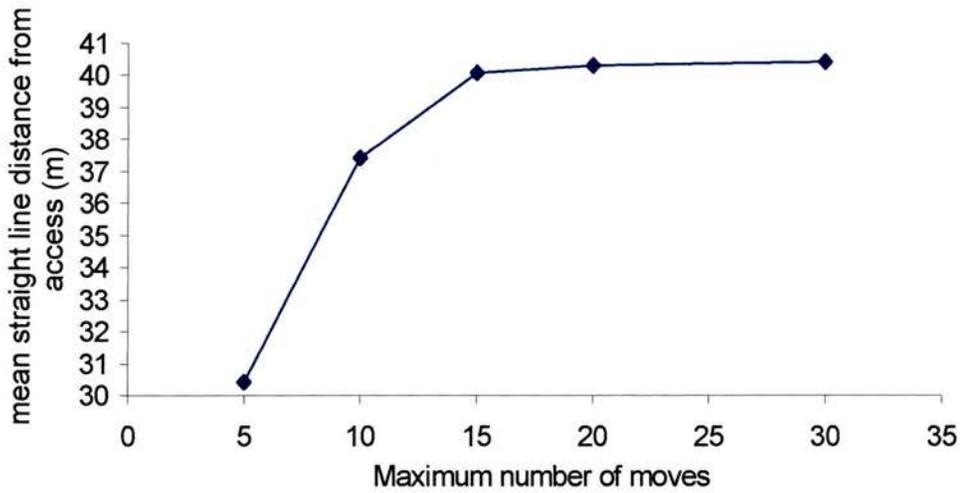


(a)

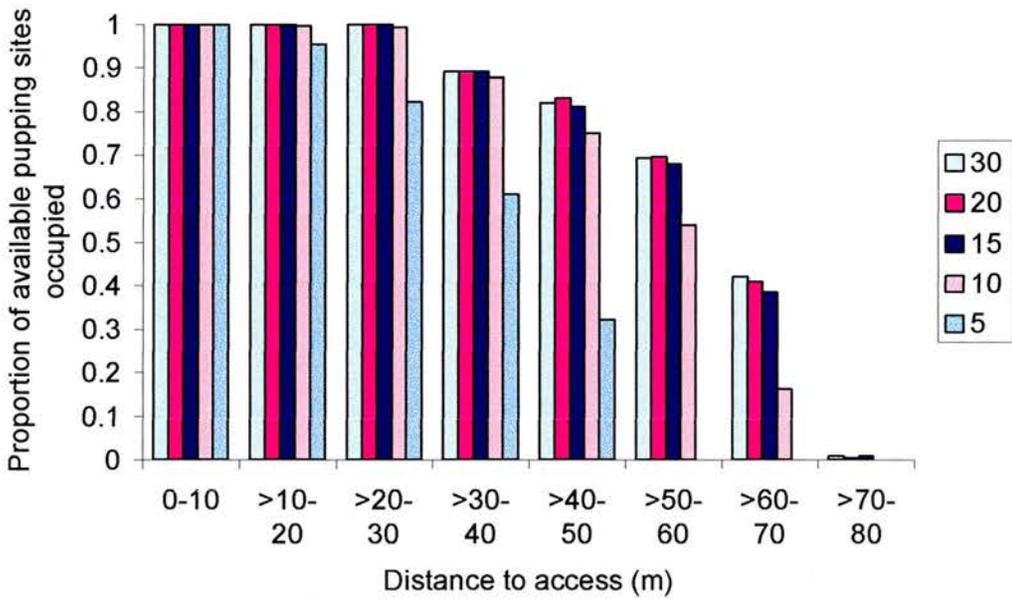


(b)

Figure 2.3.3: The mean distance to access (a) and the proportion of available pupping sites at each distance interval occupied by seals (b) when the number of possible moves varies between 5 and 40 moves and 150 seals arrive.

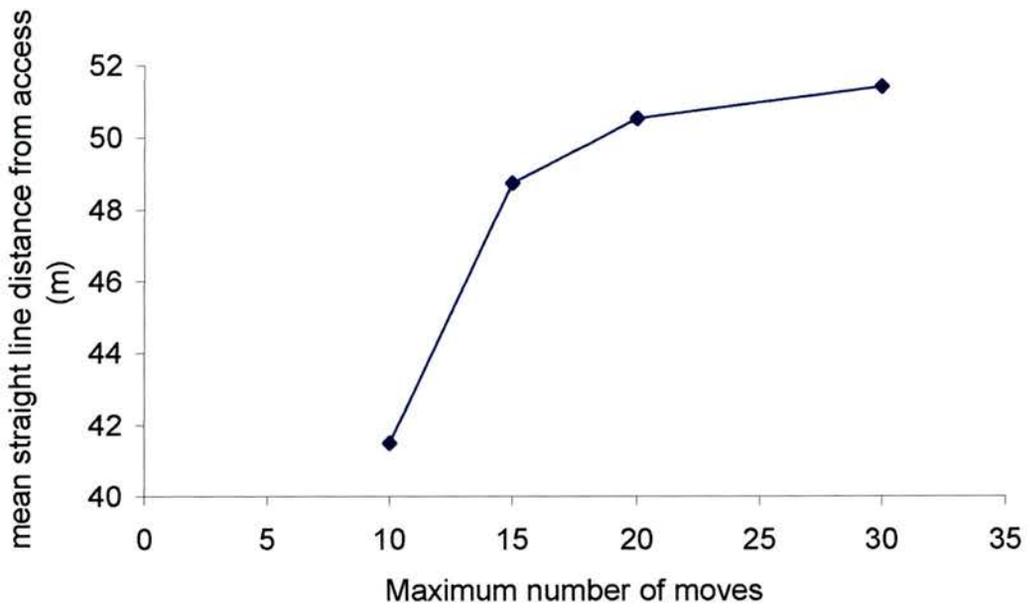


(a)

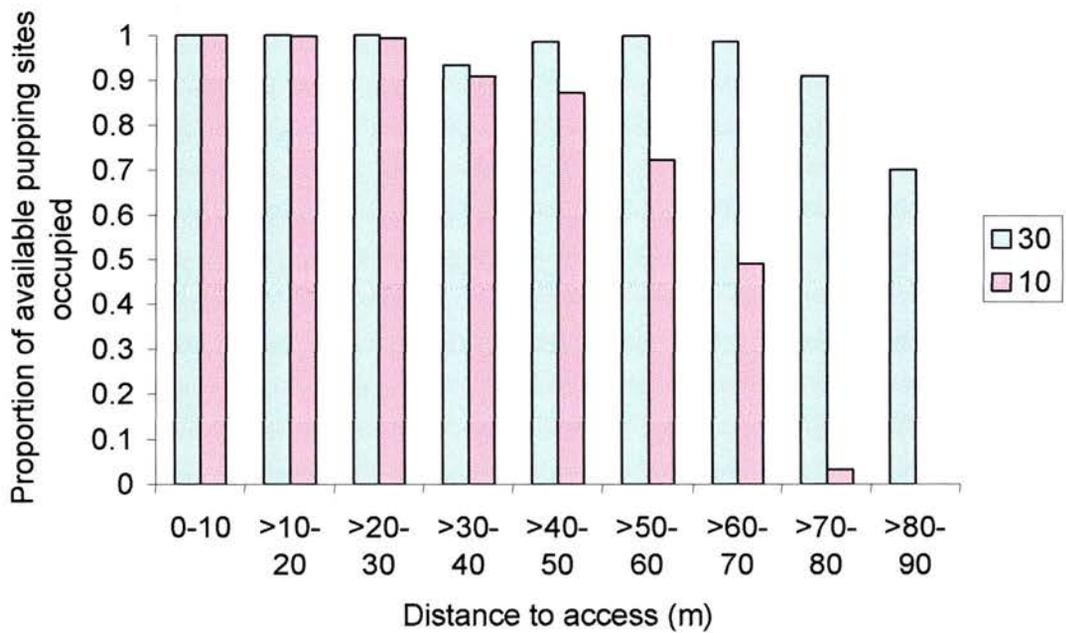


(b)

Figure 2.3.4: The mean distance to access (a) and the proportion of available pupping sites at each distance interval occupied by seals (b) when the number of possible moves varies between 5 and 30 moves and 300 seals arrive.



(a)



(b)

Figure 2.3.5: The mean distance to access (a) and the proportion of available pupping sites at each distance interval occupied by seals (b) when the number of possible moves varies between 10 and 30 moves and 500 seals arrive.

Figure 2.3.6 shows how the distribution of seals changed during the course of the breeding season. At the beginning of the season, seals were spread evenly over all occupied cells, but towards the end of the season when many seals had left the patch, the distribution was more patchy, with some low density cells interspersed in areas of otherwise high density (Figure 2.3.6c).

Presence of additional water:

Figure 2.3.7 shows the effect of introducing a pool of water. Few seals occurred around the pool under the null model (Figure 2.3.8).

Distribution determined by distance from water:

Figure 2.3.9 shows the distribution of densities obtained when distance to water was included as a factor influencing cell choice. As the number of seals on the patch increased, new seals had to travel further to find a space. In these simulations, newly arriving seals tended to continue towards the pool rather than staying in the first available cell that they entered. Once the cells around the pool were completely occupied, the space between the access point and the pool was filled up (Figure 2.3.9b). Even later in the season, seals did not occupy cells that were a large distance from water (Figure 2.3.9c).

	39.33	48.07	48.07	48.07	50.255	54.625	61.18	69.92	78.66	87.4
	30.59	39.33	39.33	41.515	45.885	52.44	61.18	69.92	78.66	87.4
	21.85	30.59	32.775	37.145	43.7	52.44	61.18	69.92	78.66	87.4
access	8.74	24.035	28.405	34.96	43.7	52.44	61.18	69.92	78.66	87.4
access	8.74	19.665	28.405	34.96	43.7	52.44	61.18	69.92	78.66	87.4
access	8.74	19.665	28.405	34.96	43.7	52.44	61.18	69.92	78.66	87.4
access	8.74	24.035	28.405	34.96	43.7	52.44	61.18	69.92	78.66	87.4
	21.85	30.59	32.775	37.145	43.7	52.44	61.18	69.92	78.66	87.4
	30.59	39.33	39.33	41.515	45.885	52.44	61.18	69.92	78.66	87.4
	39.33	48.07	48.07	48.07	50.255	54.625	61.18	69.92	78.66	87.4

(a)

	39.33	48.07	48.07	48.07	50.255	54.625	61.18	69.92	78.66	87.4
	30.59	39.33	39.33	41.515	45.885	52.44	61.18	69.92	78.66	87.4
	21.85	30.59	32.775	37.145	43.7	52.44	61.18	69.92	78.66	87.4
access	8.74	24.035	28.405	34.96	43.7	52.44	61.18	69.92	78.66	87.4
access	8.74	19.665	28.405	34.96	43.7	52.44	61.18	69.92	78.66	87.4
access	8.74	19.665	28.405	34.96	43.7	52.44	61.18	69.92	78.66	87.4
access	8.74	24.035	28.405	34.96	43.7	52.44	61.18	69.92	78.66	87.4
	21.85	30.59	32.775	37.145	43.7	52.44	61.18	69.92	78.66	87.4
	30.59	39.33	39.33	41.515	45.885	52.44	61.18	69.92	78.66	87.4
	39.33	48.07	48.07	48.07	50.255	54.625	61.18	69.92	78.66	87.4

(b)

	39.33	48.07	48.07	48.07	50.255	54.625	61.18	69.92	78.66	87.4
	30.59	39.33	39.33	41.515	45.885	52.44	61.18	69.92	78.66	87.4
	21.85	30.59	32.775	37.145	43.7	52.44	61.18	69.92	78.66	87.4
access	8.74	24.035	28.405	34.96	43.7	52.44	61.18	69.92	78.66	87.4
access	8.74	19.665	28.405	34.96	43.7	52.44	61.18	69.92	78.66	87.4
access	8.74	19.665	28.405	34.96	43.7	52.44	61.18	69.92	78.66	87.4
access	8.74	24.035	28.405	34.96	43.7	52.44	61.18	69.92	78.66	87.4
	21.85	30.59	32.775	37.145	43.7	52.44	61.18	69.92	78.66	87.4
	30.59	39.33	39.33	41.515	45.885	52.44	61.18	69.92	78.66	87.4
	39.33	48.07	48.07	48.07	50.255	54.625	61.18	69.92	78.66	87.4

(c)

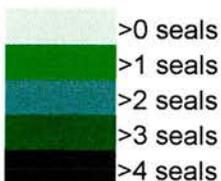


Figure 2.3.6: Null distribution on (a) day 20, (b) day 40, and (c) day 50 with 300 seals arriving over the breeding season. The distribution data is overlying a table of distance to access.

	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33

Figure 2.3.7: The mean straight line distance in metres travelled by an individual to get to water (either pool or access)

	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33

(a)

	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33

(b)

	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33

(c)

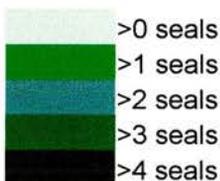


Figure 2.3.8: Null distribution in the presence of a pool on (a) day 20, (b) day 40, and (c) day 50 with 300 seals arriving over the breeding season. The distribution data is overlying a table of distance to water.

	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33

(a)

	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33

(b)

	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33

(c)

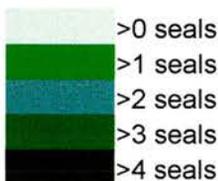


Figure 2.3.9: Distribution influenced by the presence of water on (a) day 20, (b) day 40, and (c) day 50 with 300 seals arriving over the breeding season. The distribution data is overlying a table of distance to water.

Distribution determined by distance from water and seal density:

Type 1 function

Figure 2.3.10 shows the mean densities that were observed when distance to water and the Type 1 density function were incorporated into a seal's decision of where to pup. The distribution of seals was more diffuse than observed with the null model (Figure 2.3.8) or when their distribution was influenced by the presence of water alone (Figure 2.3.9). The density of seals close to the access point and around the pool was slightly greater than elsewhere on the patch but around the pool it was lower than the density observed with either the null model or presence of water alone.

Type 2 function

The mean densities resulting from the combination of distance to water and the Type 2 density function are shown in Figure 2.3.11. The aggregation of seals around the pool was more marked than when the presence of water model was applied (Figure 2.3.9), with a lower density of seals in cells more than 10m from water.

Type 3 function

The Type 3 density function combined with distance to water produced the distribution of mean densities shown in Figure 2.3.12. This is similar to the distribution obtained with the null model (Figure 2.3.8). Seals aggregated around the access point and there was little movement towards the inland pool of water.

	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33

(a)

	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33

(b)

	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33

(c)

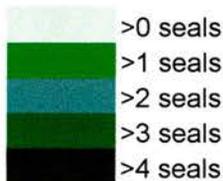


Figure 2.3.10: Distribution influenced by the presence of water and the Type 1 density function on (a) day 20, (b) day 40, and (c) day 50 with 300 seals arriving over the breeding season. The distribution data is overlying a table of distance to water.

	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33

(a)

	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33

(b)

	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33

(c)



Figure 2.3.11: Distribution influenced by the presence of water and the Type 2 density function on (a) day 20, (b) day 40, and (c) day 50 with 300 seals arriving over the breeding season. The distribution data is overlying a table of distance to water.

	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33

(a)

	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33

(b)

	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	19.665	26.22	17.48	8.74	pool	8.74	17.48	26.22	34.96
access	8.74	24.035	26.22	17.48	8.74	8.74	8.74	17.48	26.22	34.96
	21.85	30.59	26.22	21.85	21.85	21.85	21.85	21.85	26.22	34.96
	30.59	39.33	30.59	30.59	26.22	26.22	26.22	30.59	30.59	34.96
	39.33	39.33	39.33	39.33	34.96	39.33	34.96	39.33	39.33	39.33

(c)

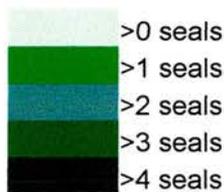


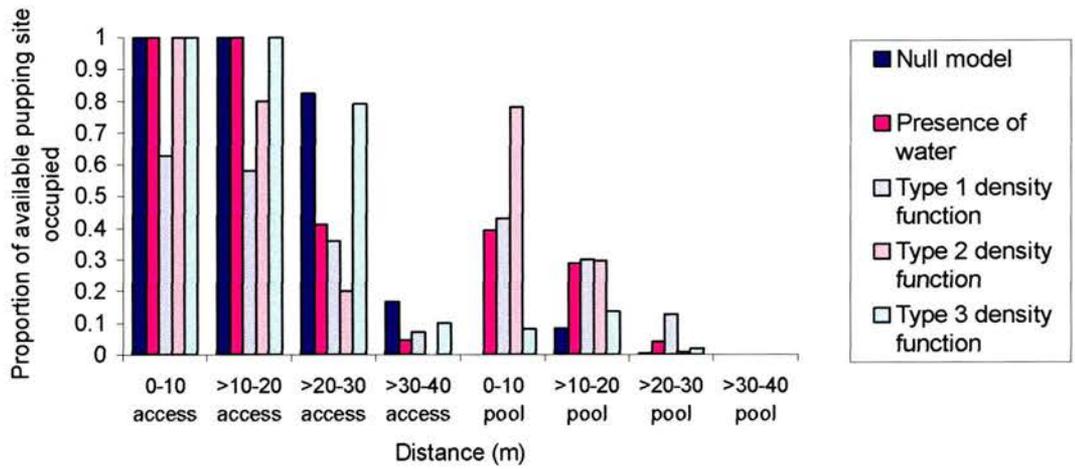
Figure 2.3.12: Distribution influenced by the presence of water and the Type 3 density function on (a) day 20, (b) day 40, and (c) day 50 with 300 seals arriving over the breeding season. The distribution data is overlying a table of distance to water.

Proportions of available pupping sites that were occupied:

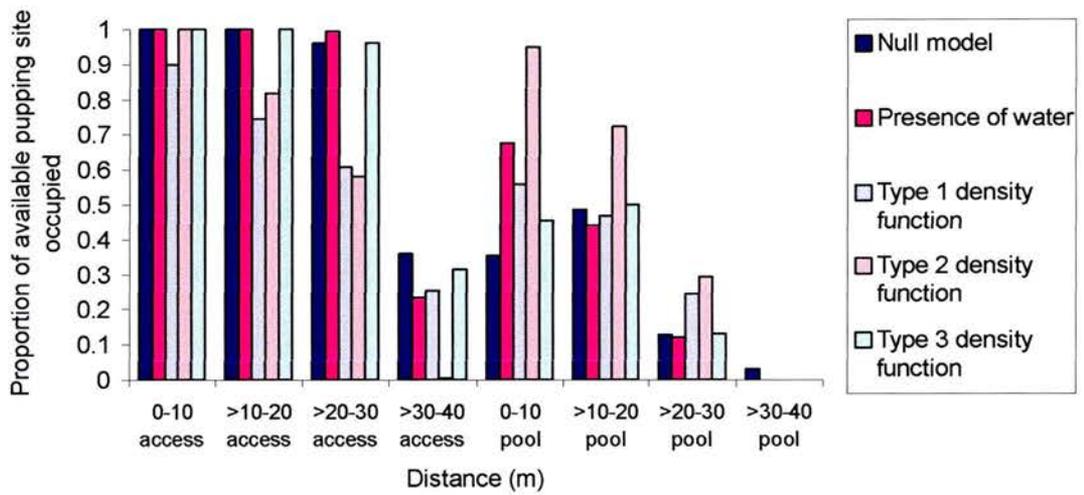
With the exception of the Type 1 density function, all pupping sites up to 10m from water were occupied (Figure 2.3.13). More of the cells around the pool were occupied when the Type 2 density function and the presence of water model was used than in any other case. Few pupping sites greater than 30m from water were occupied under any of the models.

Comparison of distributions obtained under the different models:

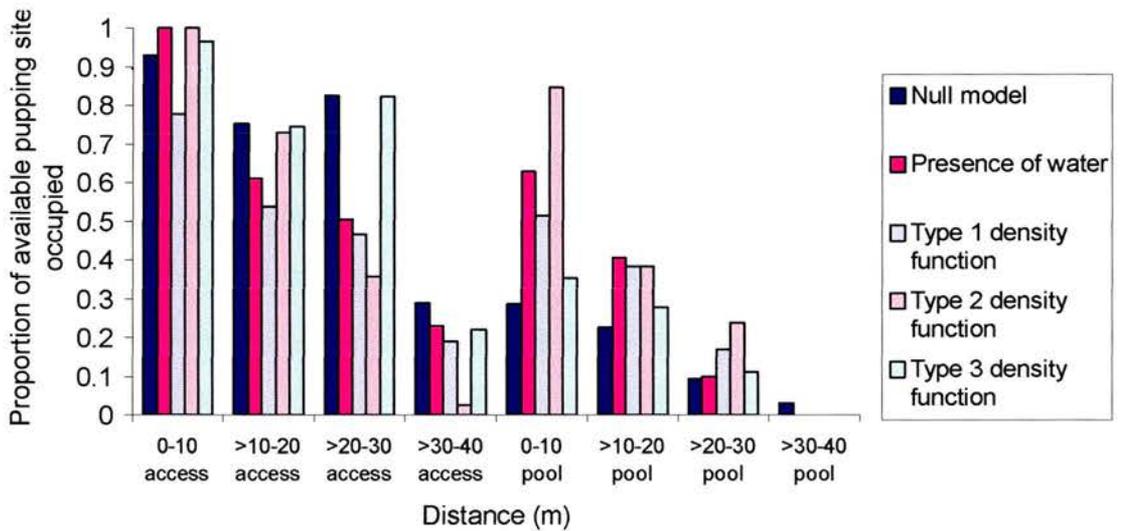
The number of matches between replicates of the null model was high (Figure 2.3.14). The combination of the Type 1 density function and distance to water produced the greatest differences from the null model with only around 20% of cells matching. The Type 2 density function and presence of water combined produced distributions that were more similar to the null model distributions. On days 40 and 50 the presence of water alone and combined with the Type 3 density function produced distributions similar to each other and to the null distributions.



(a)

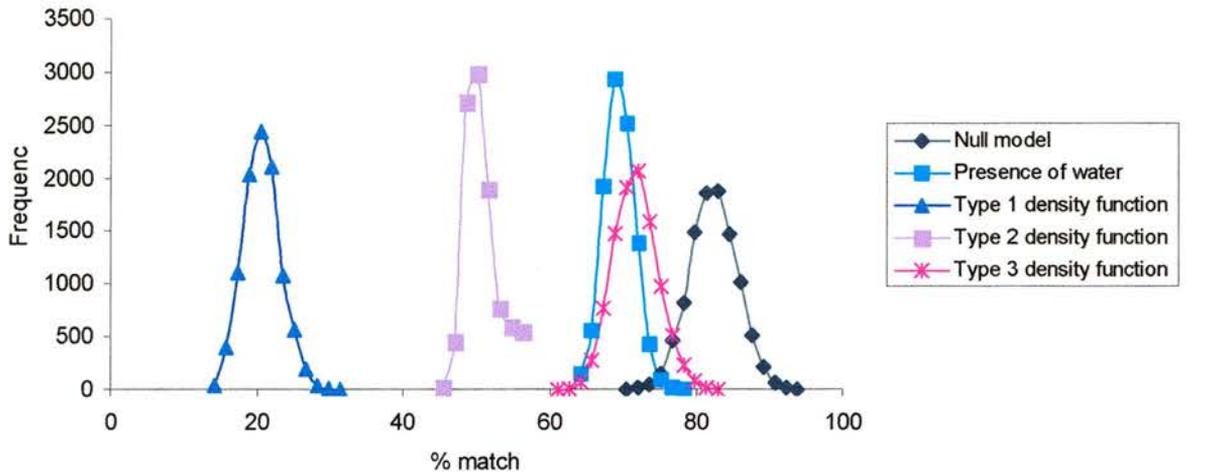


(b)

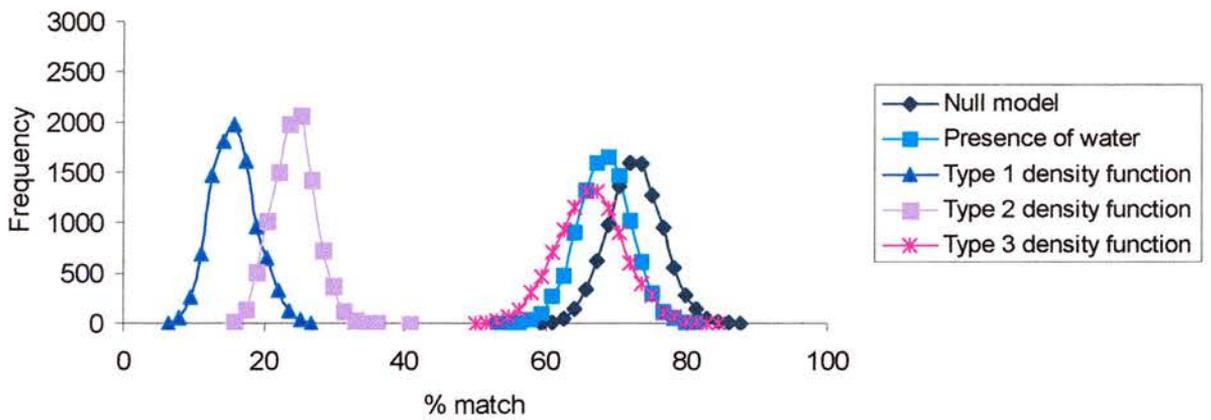


(c)

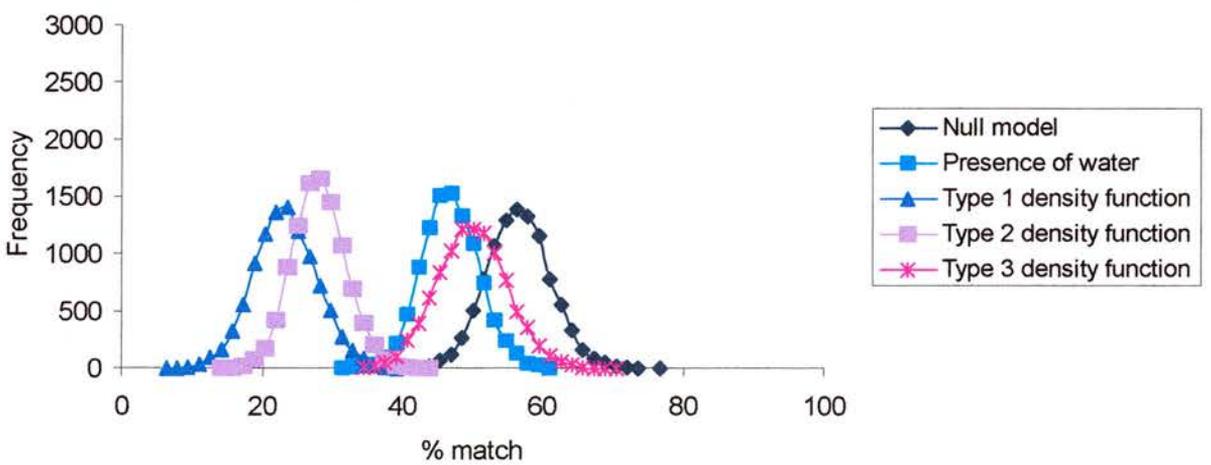
Figure 2.3.13: Proportion of available pupping sites occupied at difference distances to water (access or pool) under each simulation model on (a) day 20, (b) day 40, and (c) day 50.



(a)



(b)



(c)

Figure 2.3.14: Performance of four different models, compared to the performance of the null model on (a) day 20, (b) day 40 and (c) day 50. Performance was measured by recording the number of times a particular model achieved a specified % level of matching with the null model.

The majority of spread models have been developed to predict the spread of invasive species, for example the muskrat, *Ondatra zibethicus*, or species that are recovering from exploitation, for example the sea otter, *Enhydra lutris* (Williamson, 1996). These models are concerned with predicting the overall geographical spread of the population, which is dependent on factors such as fecundity and survival. In this study, only spread over the available breeding habitat during a breeding season is of interest. Therefore, the overall growth rate of the population is not a required parameter, instead the rate of pup production within the period of the breeding season is required. This can be estimated for each breeding patch from the counts of pups that are made from aerial survey photographs on four or five occasions each breeding season. Knowing the rate of pup production for a patch allows the presence of other seals to be taken into consideration and therefore a density regulating mechanism incorporated. In the simulations that were carried out here, the arrival of females (and therefore pup production) mimicked the shape of pup production curves that have been estimated from the aerial survey pup counts.

When distance to water was allowed to affect the choice of pupping site, fewer seals were found more than 35m from access and more seals were found within 10m of the pool compared to the null distribution. When the density of conspecifics was combined with topography in three varying functions, the resulting distributions were all different. A more diffuse distribution, with few cells containing more than four seals, was obtained when the choice of pupping site was a linear function of distance to water and seal density. When pupping site choice was affected by

distance to water and high densities of seals, fewer seals were observed at distances greater than 25m from access and more seals were observed within 10m of the pool compared to any other model. Allowing seals to be attracted to cells with moderate densities of other seals produced distributions that differed little from the null distribution.

These simulations demonstrate that it should be possible to use the observed distribution of grey seal pups in aerial photographs to identify the most important factors determining the choice of pupping sites by female grey seals. All of the models used in these simulations produced distributions of pups that overlapped very little with that predicted by a simple diffusion model. The greatest differences were observed around pools of water and in the area between the access point and the pool, particularly towards the start of the breeding season when relatively few seals were present.

Chapter 3

Development of a Method for the Extraction of Distributional and Topographical Information from Aerial Survey Photographs.

3.1 Introduction

Since 1963, the Sea Mammal Research Unit (SMRU) has carried out annual aerial surveys of the main grey seal breeding colonies around Scotland to generate a population estimate based on pup production. The Natural Environment Research Council (NERC) has a statutory obligation to provide the Department of Environment, Food, and Rural Affairs (DEFRA), and the Scottish Executive (SE) with scientific advice relating to the management of seals under the Conservation of Seals Act 1970 and related Orders (Harwood, 1997). The SMRU provides the NERC Special Committee on Seals (SCOS) with annual estimates of pup production and associated total population size that allow SCOS to advise DEFRA and the SE on management issues.

The most reliable of these surveys began in 1985 when an image-motion compensation device (Hiby *et al.*, 1988) that made it possible to use high-resolution colour aerial photography (Hiby *et al.*, 1987) was introduced. Although the use of colour film makes discriminating between animals and background objects easier and more accurate, the low ambient light levels during the grey seal breeding season made it impossible to use this format until image-motion compensation was implemented. The camera lens is pre-focussed to a mean survey height of 366m and this provides a spatial resolution of approximately 2cm on the ground (Duck *et al.*, submitted). The area of overlap between images must be delineated to avoid double-counting any pups in the area of overlap. A microfiche reader is used to view the

transparencies at the high magnification (x22) required to count the pups present (Hiby *et al.*, 1988). The spread of pupping dates at each colony exceeds the length of stay of individual pups so no individual survey will include all the pups born (Harwood, 1997; Ward, 1987). Therefore a series of surveys of each colony has to be conducted within one breeding season. In recent years most colonies have been surveyed at least four times in order to estimate all the parameters of the birth curve (Duck *et al.*, submitted).

The current method used to extract counts from the transparencies is accurate and cost-effective. However, the availability of high-resolution scanners, GIS technology and large computer hard disks has opened up opportunities for extracting additional information from the photographs of the breeding colonies.

Understanding more about the distribution of grey seals on a breeding colony may allow us to define what is suitable breeding habitat. It is clear that all of the terrain on the islands that have been colonised to date is not equally suitable for use by breeding seals. Some areas of a colony are occupied by seals at relatively high densities whereas surrounding areas are empty. These discrete areas of relatively high density will be referred to from now on as “patches”, following Gilpin and Hanski’s (1991) definition of a patch as “the area of space within which a local population lives”, where a local population is “the set of individuals which all interact with each other with a high probability”. Pupping sites are locations within the patch at the scale of an individual. If we are to discover what limit the number

of suitable habitable patches places on species abundance, we need to be able to identify and measure those habitable patches that are currently vacant (Begon *et al.*, 1996). From this we can predict how far existing patches can spread and perhaps predict where new patches are most likely to occur. Defining suitable habitat types may also help us to understand more about local population dynamics because the number of suitable patches within a geographical region may be the ultimate determinant of local population size (Harwood and Prime, 1978). Many field studies have been carried out on a small number of grey seal breeding patches (Baker and Baker, 1988; Kovacs, 1987; Pomeroy *et al.*, 2000a; Prime, 1981; Prime, 1982; Twiss *et al.*, 2001). These ground-based studies have helped to identify the factors which might be involved in pupping site selection by a female. Pomeroy *et al.* (1994) showed that breeding females aggregate around access gullies on the North Rona breeding colony. As well as sites that have access to the sea, females also appear to prefer pupping sites close to pools of water (Twiss *et al.*, 2000a; Twiss *et al.*, 2001). This may be a behavioural adaptation to the problem of keeping cool whilst on land, as keeping the body wet may assist in controlling body temperature (Anderson *et al.*, 1975; Twiss *et al.*, 2002).

The number and size of inland pools of water on a breeding colony changes over the course of a breeding season, depending on the distribution of precipitation (Redman *et al.*, 2001). The distribution of these pools on each survey date, and thus changes in water availability, can be mapped from aerial photographs. These photographs

can also be used to obtain information on other topographical features, such as access to the sea and barriers to movement such as cliffs.

To test whether these observed preferences are consistent with occupancy patterns on other colonies, we need to be able to look at how distributions vary in relation to the underlying topography on a variety of islands within and between seasons. The use of remotely-sensed data and GIS to analyse relationships between animal distributions and landscape patterns is becoming increasingly popular (Debinski *et al.*, 1999; Donovan *et al.*, 1987). However, the present methodology used to obtain grey seal pup counts from aerial photographs does not provide information on either seal distribution or underlying topography, so a new methodology had to be developed.

Aerial photographs were digitised, rectified to real-world coordinates and tessellated with the aid of an Ordnance Survey Land-Form Panorama Digital Elevation Model (DEM) to produce a map of each colony with the areas of photographic overlap eliminated. There were a number of problems involved with this process that had to be overcome. First, the movement of the aircraft introduces error because of slight changes in the height of the camera and the camera orientation between successive photographs. Second, the aerial surveys have been conducted with only limited overlap between successive photographs (a maximum of 10%) in order to save both time and expense. As only three individuals have carried out all the pup counts since 1984 (Duck *et al.*, submitted), error caused by different individuals

misclassifying adult or juvenile seals, gulls, sheep and rocks as seal pups was minimised by repeated mapping and counting by one of the original counters.

Grey seal pups have traditionally been classified into five developmental stages (Boyd *et al.*, 1962), stage 1 to 3 pups have a white natal coat, during stage 4 pups start to moult, and by stage 5 they are fully moulted and are usually weaned. Pups start to moult at around 15 days after birth (Redman pers comm.), Duck *et al.*, (submitted) estimated that the mean time to completion of the moult is 23 days with a standard deviation of five days. If pups in aerial photographs can be classified into these stages, the resulting counts will provide more information on the number of pups born at different intervals of the breeding season.

3.2 Methods

The grey seal breeding colonies in Orkney, Scotland (Figure 3.2.1) are ideal sites at which to study grey seal colony expansion and development. The colonies in Orkney have shown the biggest increase in pup production over the last three decades and it is of interest to see in which areas there remains the potential for further increase. Also, very few detailed field studies of breeding grey seals have been carried out in Orkney. Ten colonies were selected (Table 3.2.1) as potential areas of interest because of the different stages they represent in the colonisation process and for their differing topography.

Before information on the positions and densities of grey seals could be extracted, the aerial photographs had to be digitised, rectified to real world coordinates and tessellated (see Appendix 2 for detailed methods).

Digitising photographs:

Most photogrammetric cameras introduce fiducial marks onto every photograph. A fiducial mark is a position on the photograph that can be pinpointed on the scanned image. Measurements of the distance from the centre of the scanned image to these marks can be compared to the calibrated coordinates of the fiducial marks to correct for any distortions from the scanning process. However, the Linhoff Aerotechnica camera used by the SMRU for aerial surveys is not a true photogrammetric camera and does not produce such marks, which had to be added to the photographs by hand. The centre of each photograph and eight additional points around the centre

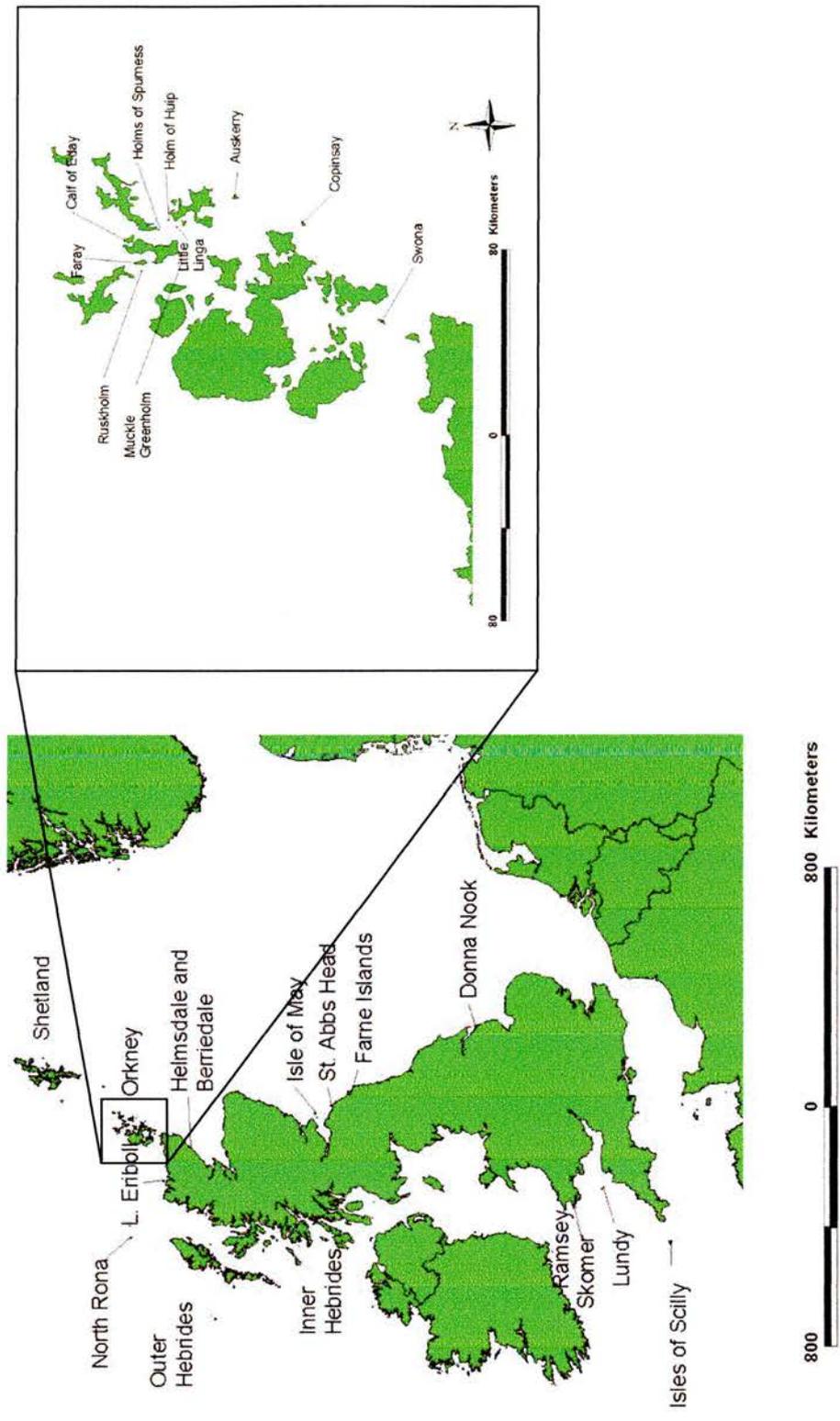
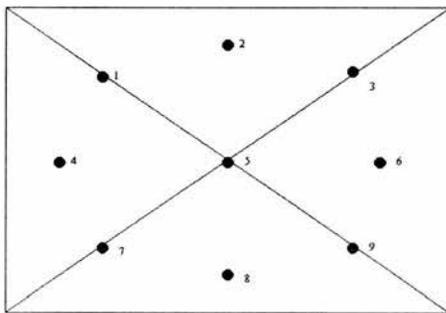


Figure 3.2.1: Grey seal breeding colonies around the UK and the chosen study colonies in Orkney.

Table 3.2.1: The 10 Orkney islands chosen for study.

Island	Status	Pup production in 2001
Swona	Increasing	1077
Holm of Huip	Increasing	1402
Muckle Greenholm	Increasing	1000
Copinsay	Increasing	2540
Calf of Eday	Increasing	556
Faray	At equilibrium	2168
Holms of Spurness	At equilibrium	482
Ruskholm	At equilibrium	239
Little Linga	At equilibrium	482
Auskerry	Decreasing	58

point were chosen as fiducial points (Figure 3.2.2a). The coordinates of each point were measured in millimetres from the centre point (Figure 3.2.2b). All the photographs are the same size (12.7cm x 10.16cm) therefore the measurements were made only once and a template was created. Pinholes were added to each photograph to mark the positions of the fiducial marks. The photographs were then scanned using a Polaroid SprintScan 45 scanner at a resolution of 2540 dpi.



(a)

Point	X coordinate	Y coordinate
1	-32.3	40.3
2	-2.3	50.3
3	27.7	40.3
4	-42.3	0.3
5	0	0
6	37.7	0.3
7	-32.3	-39.7
8	-2.3	-49.7
9	27.7	-39.7

(b)

Figure 3.2.2: The positions on the photograph (a) and coordinates (b) of the fiducial marks.

Ground control point collection:

Rectification is the process of transforming data from one grid system to another, for example from pixels into a map coordinate system. For accurate rectification, an accurate set of ground control points (GCP) is essential. From the GCPs, the rectified coordinates for all other points in an image are extrapolated. A good quality set of aerial photographs was colour-photocopied and laminated for each study site. At least four easily identifiable, permanent objects, to be used as GCPs

were located on each photograph. During the summer of 2000, the British National Grid (BNG) locations and the altitudes of these GCPs were recorded using a differential geographical positioning system receiver (Garmin 12xl).

Rectification of the scanned images:

Orthorectification involves the incorporation of a DEM into the rectification process to correct for terrain displacement (ERDAS, 1999). The orthorectification software used in this study was ERDAS Imagine V8.3.1. Imagine Orthobase produces orthorectified images in which the displacement of objects due to camera orientation, terrain relief and other errors has been removed. The rectified image has the geometric characteristics of a map with the image qualities of a photograph. Thus, any measurement taken on a rectified image will be an unbiased estimate of an equivalent measurement taken on the ground. Individual rectified images can then be tessellated, or stitched, together to form a base map.

First, the images had to be corrected in both their interior and exterior orientation. Interior orientation defines the internal geometry of the camera as it existed at the time of data capture (shutter release). The variables associated with image space are primarily used to transform the image pixel coordinate system to the image space coordinate system.

The interior orientation was defined by first stating the focal length of the camera (150mm), which is the length from the principal point to the perspective centre

(Wang, 1990), where the principal point is the intersection of the perpendicular line through the perspective centre of the image plane (Figure 3.2.3). The image position of the principal point had to be determined for each image using the fiducial marks (Figure 3.2.3). The position of each fiducial mark was located on each scanned image and the coordinates entered into ERDAS Imagine.

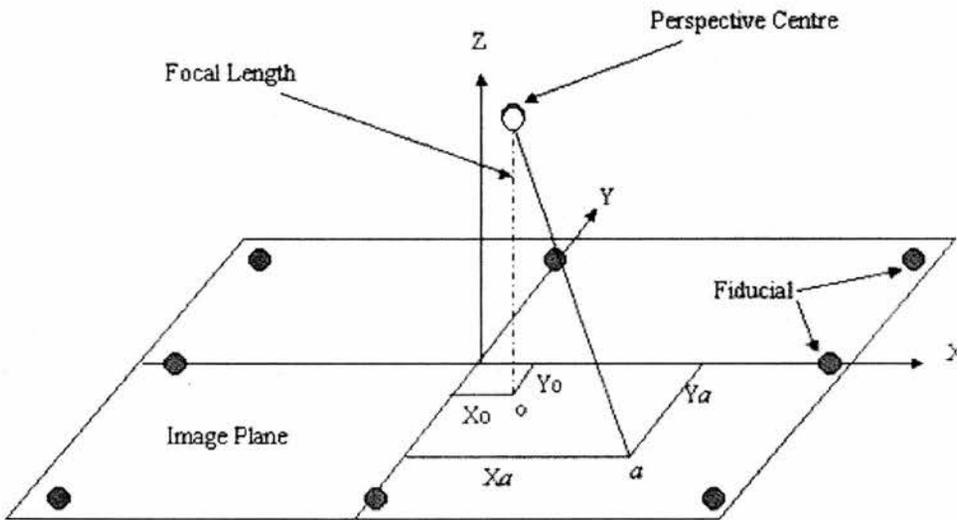


Figure 3.2.3: The internal geometry of an image illustrating the variables associated with data capture, where 0 represents the principal point and a represents an image point (after ERDAS, 1999).

Exterior orientation defines the position and angular orientation associated with an image. The elements of exterior orientation define the characteristics associated with an image at the time of exposure or capture. As many ground control points as possible were identified on each scanned image and their British National Grid coordinates and altitudes were entered into ERDAS Imagine. Due to variable tidal

conditions, it was not always possible to identify the full complement of ground control points on each set of images. In addition to the ground control points, tie-points were located in the areas of overlap between adjacent images. Tie-points do not have known coordinates associated with them but they identify objects that can be seen in two or more images. The angle of the flight path in relation to the direction of true North (κ) was also determined using the flight path records that are made during each survey.

Triangulation, orthorectification and tessellation of the rectified images:

Once the interior and exterior information had been entered into ERDAS Imagine, the images were triangulated. Triangulation involves calculating the exterior orientation parameters associated with all the images and determining the x, y and z coordinates of the tie-points. The results of the triangulation were accepted when the total root mean square error (RMSE) was lower than 2. The RMSE is the distance between the input location of a GCP and the estimated location of the same GCP after the geometric transformation (ERDAS, 1999). A total RMSE of 2 represented a compromise between accuracy and time spent on each set of photographs. Inaccurate ground control points and tie-points were identified in the triangulation report and eliminated. The images were then orthorectified using the Ordnance Survey Land-Form Panorama DEM for the relevant island (see Appendix 1 for details of how to create a continuous DEM surface). The resulting orthorectified images were opened in the ERDAS viewer and overlaid on each other to form a map. This map was checked for inaccuracies by making measurements of

the distance between three pairs of objects that were visible in each area of overlap between adjacent images. The mean overlap error and its standard deviation were calculated for each survey of each colony.

Extraction of topographic information and pup distributions:

The base map was opened in the ERDAS viewer, and a vector layer was created for each desired characteristic. Separate polygon vector layers were created for the coastline, taken as the midpoint between mean high water and mean low water, and the inland pools of water. A line vector layer was created to depict barriers to movement such as cliffs. Point vector layers were created for the positions of each pup. A point vector layer was created for each pup stage. All vector layers were saved as shapefiles so that they could be used with ArcView 3.2 (ESRI).

Three different pup stage categorisations were used. In order to investigate where females choose to give birth, the locations of only those pups in stages 1 to 3 (white-coated pups) were mapped. These stages were chosen because pups in stages 4 and 5 often move away from their birth site, whereas younger pups are less likely to move. In order to compare the counts from the scanned images with those obtained by using a microfiche reader and the original photographs, the locations of all pups of stages 1-4, and stage 5 (fully-moulted pups) were also mapped.

The ArcInfo 8.1 (ESRI) function, "Pathdistance" was used to calculate the distance to water and access to the sea of every point on a colony using the positions of the

coastline and pools of water extracted from the images (see Appendix 3 for ArcInfo 8.1 code). Only one distance to access surface was generated for each island, but a different surface for distance to water had to be created for each survey date because of varying precipitation rates both within and between breeding seasons.

The vector layers for coastline, pools of water and barriers to movement were first converted to grid layers in ArcView 3.2 at a resolution of 2m x 2m. The coastline and pools of water grids were merged to produce a grid of all available water sources. The Pathdistance function calculates the minimum accumulative travel cost from a source, either water or access, to each cell location in a grid whilst compensating for both the actual surface distance travelled and the vertical factors influencing the total cost of moving from one location to another. Other potentially important factors (eg. wind speed and direction) that can be included in the Pathdistance calculations were not included in this study because they are not relevant to seal movement. I used the same weightings for slope as Twiss *et al* (2000a) to calculate the cost surfaces (Figure 3.2.4). Negative slopes were modelled by the cosine function, which implies that there is an advantage to travelling over slight to moderate downhill slopes. Positive slopes were modelled by the secant function, implying that the cost of locomotion increases with the slope. Values obtained using these functions were raised to the power of two to give the final vertical factor values. For any slope in excess of 84° the vertical factor was set to infinity, implying that this is an impenetrable barrier to movement.

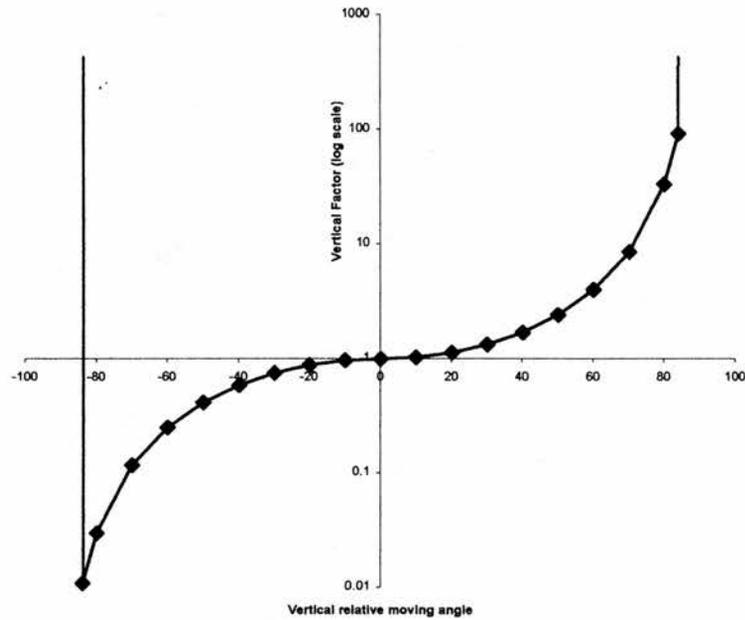


Figure 3.2.4: The cosine-secant vertical factor graph used to model the cost for a seal of moving over a surface of varying elevation.

The input surfaces were a source grid, a cost grid, a surface grid and a vertical factor grid. The source grid was either the coastline grid (for calculating the distance to access surface) or the combined coastline and pools of water grid (for calculating the distance to water surface). The cost grid includes any barriers to movement such as cliffs. The surface grid was an interpolated grid calculated from the OS Land-Form Panorama DEM. The surface grid allows the actual distance between cells to be calculated. Given the cell size and the z-value for each cell, the surface distance between any two cells can be calculated using Pythagoras' theorem. The DEM was also used to calculate the slope between any two cells so that the cost of moving between them could be calculated.

The surfaces were exported to ArcView 3.2 and the positions of the white-coated pups overlaid on them so that the relationship between distance to water, distance to access and slope and pup locations could be examined visually.

3.3 Results

For the purposes of illustration only the results from Cornholm in 1999 are presented here. Cornholm (58°54'N, 2°42'W) is a small island that was first colonised by breeding grey seals in the early 1990's. It was first surveyed by SMRU in 1993.

The accepted RMSE varied slightly between the survey dates (Table 3.3.1). After orthorectification, the tessellated images were overlaid to create a base ortho-image of the island (Figure 3.3.1) from which the topographic and distributional data was extracted (Figure 3.3.2). The average error in the overlap between images for each date is given in Table 3.3.1. As the accepted RMSE increases the resulting average overlap error increases.

Table 3.3.1: The accepted RMSE for orthorectification and the resulting overlap errors in the base map for each date.

Survey Date	Root Mean Square Error (RMSE)	Average overlap error (m), standard deviation and sample size
16 October 1999	1.57	7.828 ± 4.27 (n=24)
11 November 1999	0.854	3.366 ± 2.3 (n=30)
29 November 1999	0.9082	5.354 ± 2.63 (n=21)

Counts extracted from the tessellated image and the microfiche reader were highly correlated (Figure 3.3.3, $R^2=0.9642$), although the microfiche counts of white-coated pups were generally lower than the counts from the tessellated image, whilst the microfiche counts of moulted pups were slightly higher than the counts from the

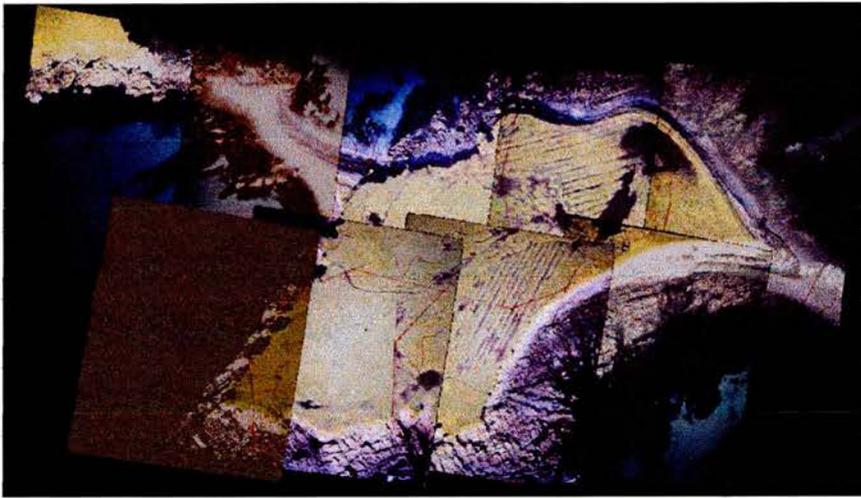


Figure 3.3.1: The ortho-image of Cornholm, Orkney on the 11 November 1999.

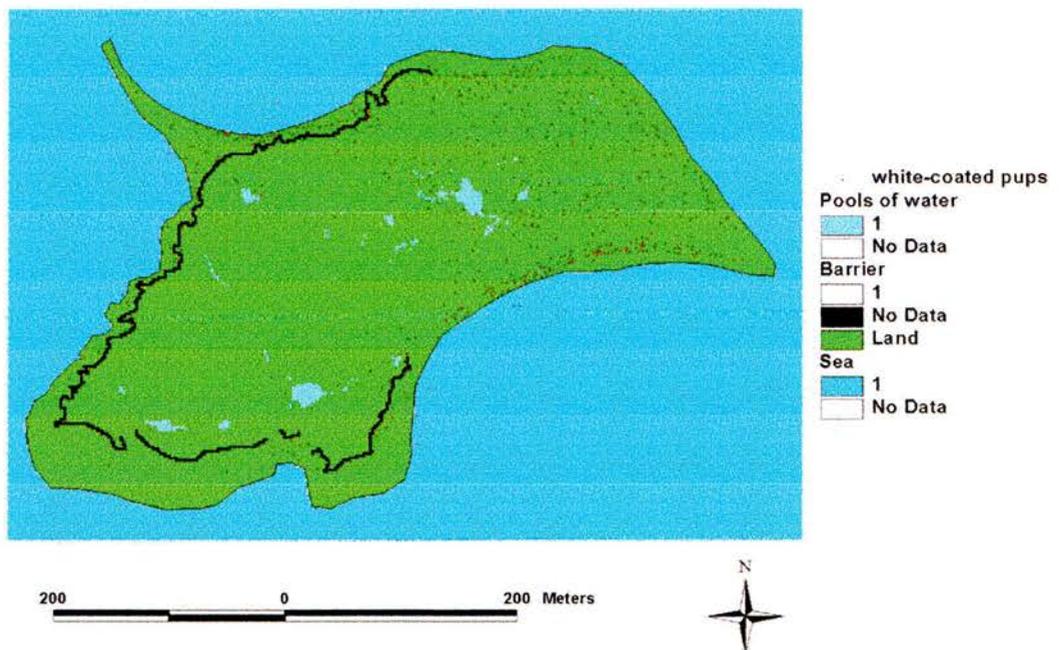


Figure 3.3.2: The extracted coastline, pools, barriers to movement and positions of white-coated pups.

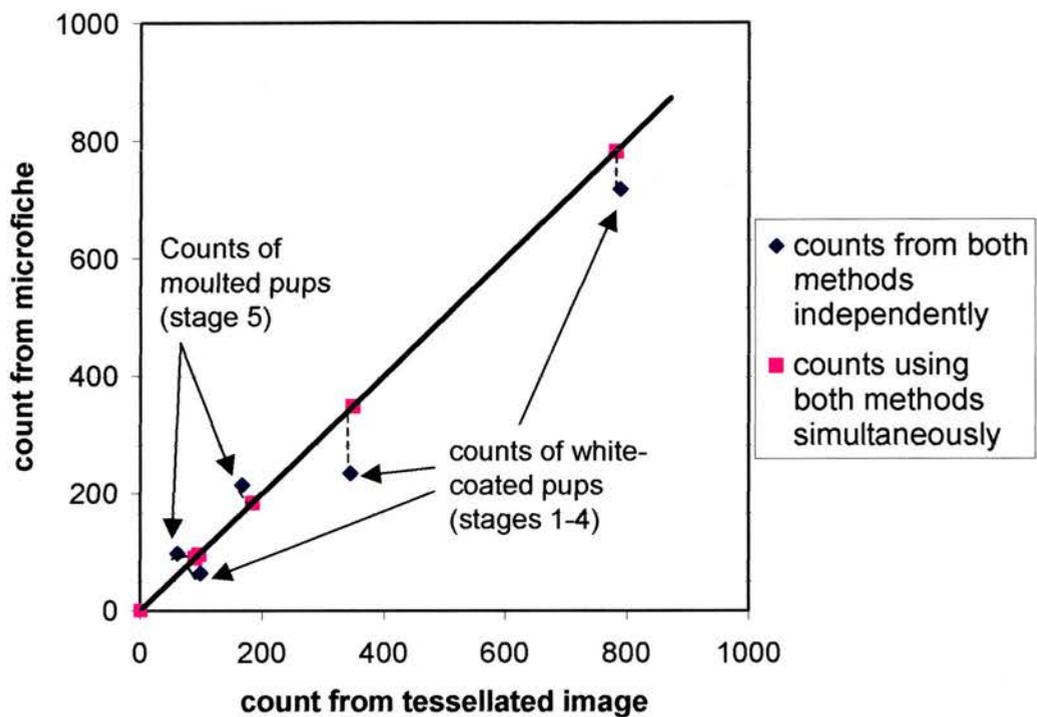


Figure 3.3.3: Comparison of counts for three photographic surveys of Cornholm in 1999 made by an experienced aerial survey counter using the original photographs, the tessellated digital image, and both sources simultaneously. The solid line represents what would be expected if the counts were identical. The dashed line links the counts made from the same set of photographs using the methods independently and simultaneously.

tessellated image. An additional set of counts was performed using both the microfiche reader with the original photographs and the digitised image simultaneously. This gave counts that were higher than those obtained using either source on its own for white-coated pups and lower counts for moulted pups (Figure 3.3.3).

Counts of white-coated pups (stages 1-3) in the tessellated images made by an inexperienced counter (C Stephenson) were consistently lower than those made by an experienced counter (C Duck, SMRU). The greatest difference between the counts was on 29 November 1999 (Figure 3.3.4). To test if this difference was the result of misidentification of white-coated and moulted pups, images from the 16 October and 29 November were recounted by the inexperienced counter. All pups that might have been classified as white-coats were included in these revised counts. The revised count from 16 October was only slightly greater than the previous count and was still lower than the count made by the experienced counter (Table 3.3.2). The revised count from 29 November was higher than that made by the experienced counter (Table 3.3.2).

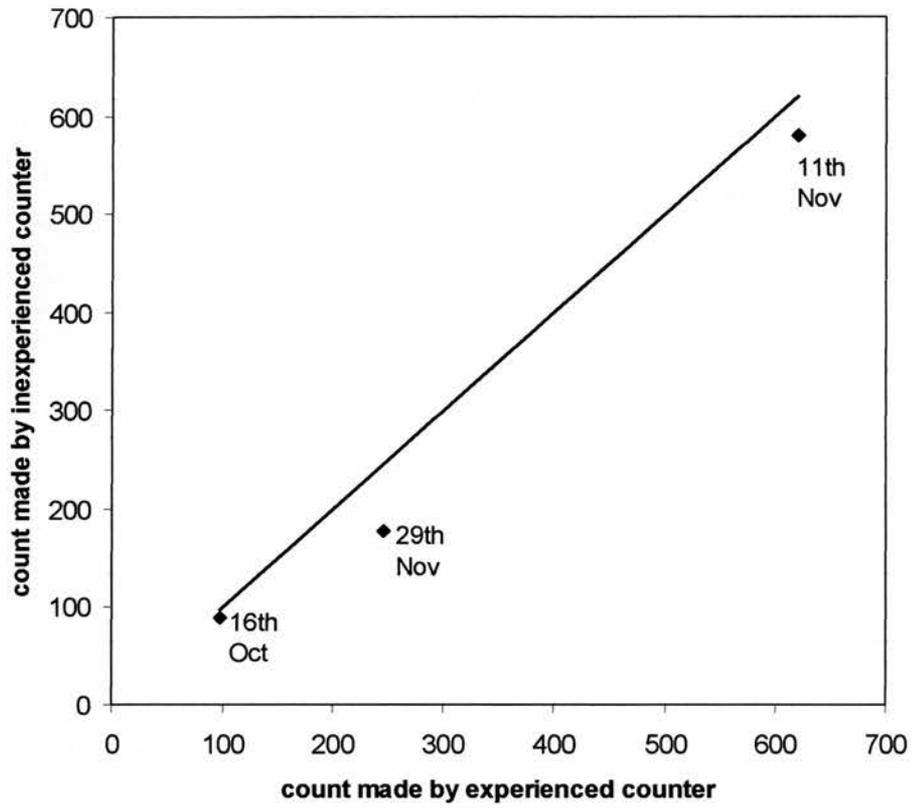


Figure 3.3.4: The counts of white-coated pups (stages 1-3) classified independently by an experienced and an inexperienced counter for the three dates in 1999. The solid line represents what would be expected if the counts were identical.

Table 3.3.2: Counts of the number of white-coated pups (stages 1-3) on Cornholm made by an experienced and an inexperienced counter for three dates in 1999.

Date	Count by inexperienced counter	Count by experienced counter	Repeated count by inexperienced counter
16 October 1999	90	98	93
11 November 1999	580	620	–
29 November 1999	178	246	321

The height, slope and distance to access surfaces for Cornholm (Figure 3.3.5 - 3.3.7) show that most of the easily accessible habitat is on the eastern half of the island, whereas access to the western side is restricted by cliffs. The maximum distance to access was approximately 230m (Table 3.3.3). A distance to water surface was generated for each survey date (Figure 3.3.8). The amount of habitat close to water increased as the season progressed and, as a result, the mean and maximum distances to water decreased over time (Table 3.3.3).

Table 3.3.3: Summary statistics of the distance to access to the sea and distance to water for potential pupping sites on Cornholm in 1999.

		Minimum	Mean	Maximum
Distance to access to the sea (m)		1.9	67.4	229.7
Distance to water (m)	16 October 1999	1.9	39.3	120.1
	11 November 1999	1.9	23.0	78.2
	29 November 1999	1.9	18.0	78.2

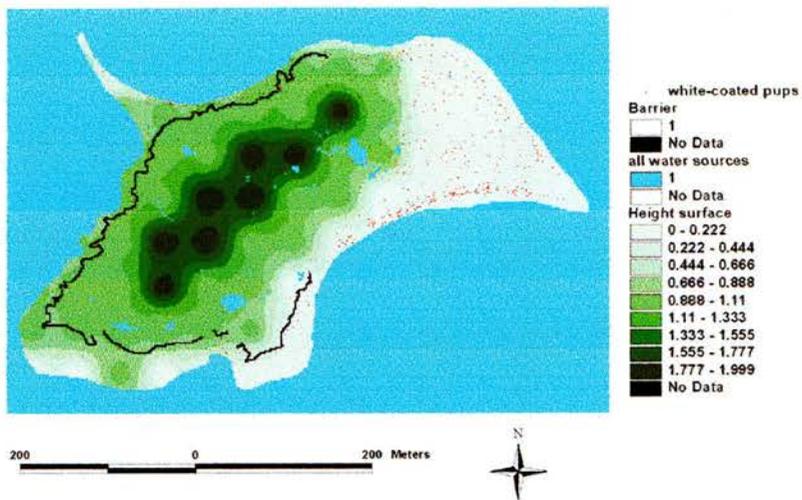


Figure 3.3.5: The DEM height surface for Cornholm.

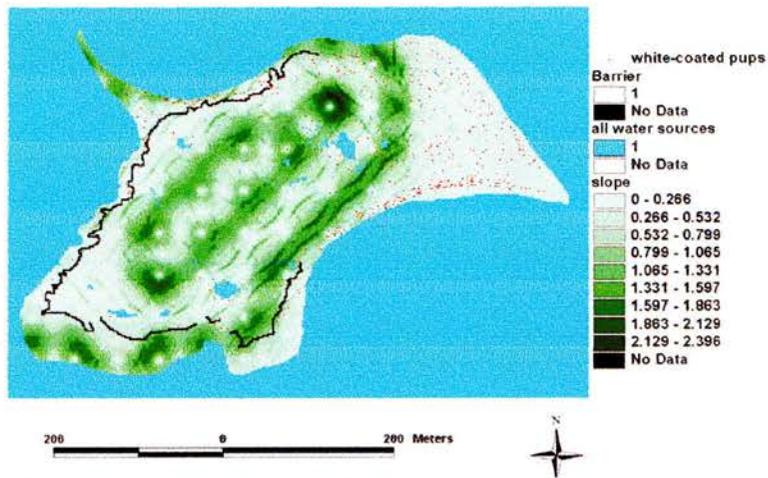


Figure 3.3.6: The slope surface for Cornholm.

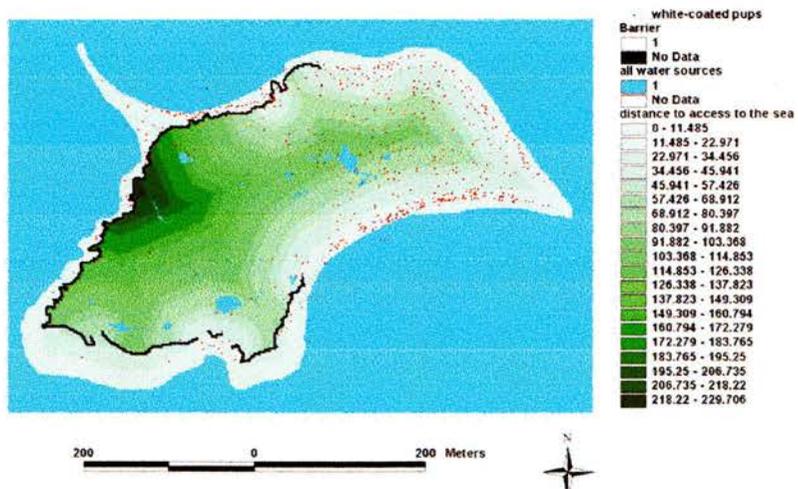


Figure 3.3.7: The distance to access surface for Cornholm.

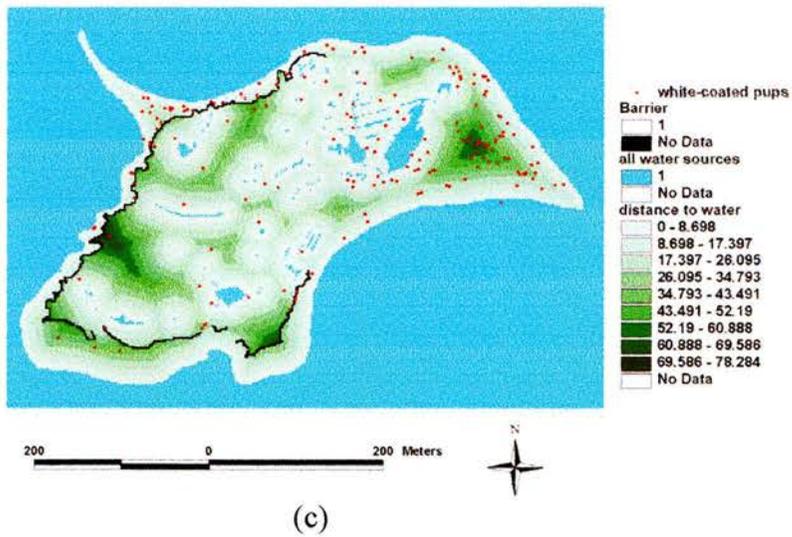
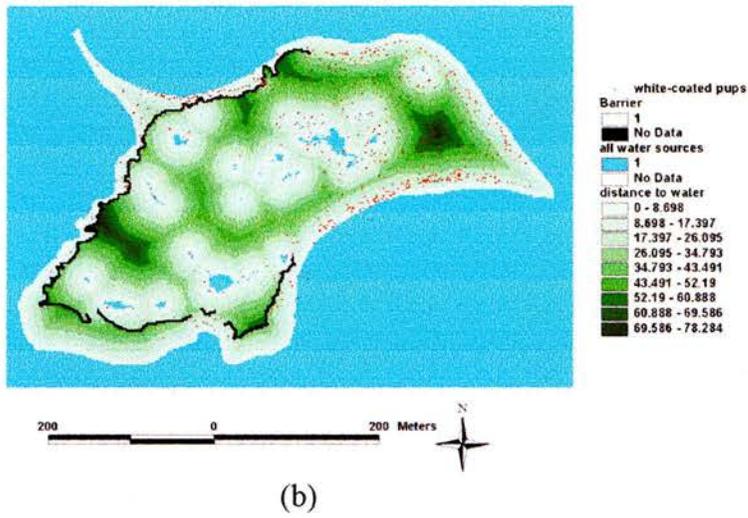
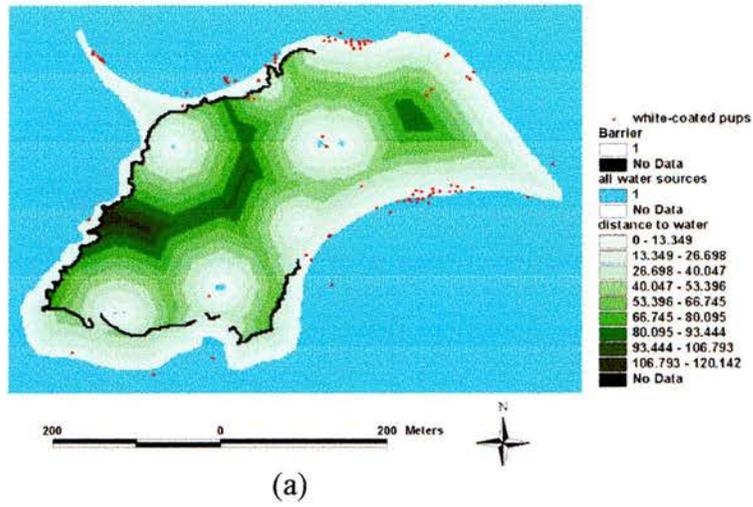


Figure 3.3.8: The distance to water surfaces for Cornholm on (a) 16 October 1999, (b) 11 November 1999 and (c) 29 November 1999.

3.4 Discussion

The current methodology used to survey the British grey seal pup production provides most of the information necessary for estimating population size on an annual basis. The method described in this chapter allows additional information on the distribution of animals within patches to be extracted from current and historical survey material. However, the accuracy of the positional information is compromised because the surveys were not designed for this purpose.

The lack of fiducial marks on the photographs and the limited overlap between adjacent photographs made the stitching process considerably more time consuming than it otherwise would have been. This problem was exacerbated by the relatively low resolution of the DEMs that were available. In order to overcome this latter problem, a fine-scale DEM of each patch would have to be constructed. This would involve carrying out a dedicated photogrammetric aerial survey that would generate a full set of stereo-paired images of each colony. Until such a survey is carried out, the only way to construct an accurate DEM on a fine-scale is to follow the method used by Mills *et al* (1997), but this is a very labour intensive procedure that has only been carried out on very small areas.

The value of the RMSE determines the error in the overlap between images, and this affects the risk of omitting or double-counting seals (Table 3.3.1). ERDAS recommend that acceptable RMSE be determined by the end use of the data. From this study I suggest a RMSE lower than 1 be reached before accepting the

triangulation transformation but due to differences in photograph quality, brightness and ability to locate ground control points this was not always possible.

The correlation between the counts made using the microfiche and the tessellated image indicates that pups can be counted effectively from the tessellated images and that the resolution of scanning is sufficient to identify pups easily against a variety of backgrounds. Most of the differences between the counts made by an experienced and inexperienced counter were due to differences in the criteria used to classify pups as white-coated (stages 1-3) or moulted (stages 4-5) pups. These effects were most pronounced at the end of the breeding season, when the proportion of moulted pups is greatest. The classification of pups is made more difficult by the presence of light-coloured moulted pups, bright sunlight (which reflecting off moulted animals can make them appear white) and muddy white-coated pups (which may be mistaken for moulted pups) (Figure 3.4.1). Although experience undoubtedly improves the consistency of classification, counts of white-coated and moulted pups will probably always differ between observers irrespective of their experience. Digitising the counts provides the opportunity to count the same image repeatedly and compare classification, which is something that has not previously been possible.

The range of heights for Cornholm in the interpolated height surface (Figure 3.3.5) from the Ordnance Survey Landform DEM confirm that the calculated surface is not a true representation of the actual height of the island. Cornholm is a relatively flat,



(a)



(b)



(c)



(d)

Figure 3.4.1: Examples of white-coated and moulted pups demonstrating some of the factors that make categorisation difficult from aerial survey photographs: (a) white-coated pup, (b) muddy white-coated pup, (c) light-coloured moulted pups, (d) dark-coloured moulted pup.

low-lying island with a maximum height of 11m, but the maximum height on the interpolated surface is approximately 2m. As a result, the incorporation of the surface grid (height) and the vertical factor grid (slope) in the Pathdistance function had little effect on the calculated surfaces for distance to water and access to the sea. The inclusion of these grids will be more important for patches where relief is more variable.

Twiss *et al.* (2000a; 2001) observed that habitats close to water sources are preferred by breeding female grey seals. It is therefore important to document changes in the availability of this type of habitat during the breeding season, and in this study a new distance to water surface was calculated for each survey. There was a dramatic change in the availability of habitat close to water on Cornholm between the start and end of the 1999 breeding season (Figure 3.3.8). The mean distance to water at the end of the season was less than half that at the start of the season. Mapping out the pools of water, calculating the distances to water and analysing the relationship between water and pup positions for each survey date may explain some of the inter-season variability in pup distribution.

The combination of photogrammetry and GIS used in this chapter allowed the relationships between topography and seal distribution to be examined at a scale that had not been possible before. Studies at individual colonies have examined some of the relationships on a fine scale but it is important to establish whether or not these relationships apply to all grey seal colonies. Until a dedicated photogrammetric

aerial survey of all the grey seal breeding colonies can be completed, the process of orthorectification using ground control points and an interpolated DEM is the most cost-effective and efficient way to extract distributional and topographical information from aerial photographs of these patches.

Chapter 4

Comparison of the Topographical Factors Influencing Pupping Site Choice over Time and Space.

4.1 Introduction

At present there appear to be many suitable places still available for grey seal colonisation. To predict which of these may become colonised we need to understand the factors involved in how a female grey seal chooses her pupping site. The absence of predators (Bartholomew, 1970), availability of pupping sites close to water (Pomeroy *et al.*, 1994) and aggressive behaviour (Caudron, 1998) have all been implicated as potentially important factors in determining whether an area will be colonised and whether the patch of occupied habitat will then expand (Harwood, 1981).

The colonisation of an area of habitat can be considered in three phases: arrival and establishment; spread; and finally equilibrium (Williamson, 1996). The spread of individual grey seals across a discrete area of habitat is of particular interest because it is determined by the availability and accessibility of suitable pupping sites. The simplest mathematical description of spread is random diffusion (Williamson, 1996), the idea being that although organisms do not move randomly, the collective behaviour at the scale of the population appears random (Levin, 1992). The simulations carried out in Chapter 2 showed that incorporating factors that have been described qualitatively as defining suitable grey seal breeding habitat affect the resulting distributions sufficiently to make them distinguishable from simple diffusion. Therefore, to describe accurately the pattern of spread observed on a grey seal breeding patch, the characteristics of suitable habitat and the factors involved must be quantified.

Defining what is a suitable site within a patch is a problematic concept for both theorist and empiricist (Begon *et al.*, 1996). Most unoccupied areas in the world are unsuitable for most species, either through natural causes or human activities, but there are also areas which are intrinsically suitable but which are, as yet, unoccupied (Thomas and Kunin, 1999). Only very rarely has the identification of suitable sites been attempted. One possible method involves identifying the characteristics of occupied sites and then determining the distribution and abundance of similar sites within a patch to determine boundaries of spread (Begon *et al.*, 1996). As part of this process, the landscape can be divided into cells, each of which can then be described in terms of factors that may influence the spread (Thomas and Kunin, 1999).

Twiss *et al.* (2001) have quantified the topographical features of habitat occupied by breeding female grey seals on two breeding patches on the Isle of May, Scotland. For these breeding patches, occupied cells were closer to access points to the sea and to pools of water than unoccupied cells. They hypothesised that the preference for close proximity to water may restrict colony expansion (Twiss *et al.*, 2001). These observations may be specific to the topographical conditions found on the Isle of May but they are potentially useful for identifying management priorities on a patch where conflicts of interest are a possibility. It is not known, however, if the characteristics of occupied cells on the Isle of May breeding patches can be used to predict the spread of seals on other breeding patches around the UK. To establish the generality of these relationships, similar occupancy patterns must be observed on a range of different patches over time.

The Hebrides and Orkney are the two main breeding centres of the UK grey seal population (SCOS, 2002). Pup production in Orkney in 2000 accounted for 47% of all pups born at annually monitored sites (SCOS, 2002). Pup production in the Hebrides has been relatively constant since 1992 and Harwood and Gaggiotti (1999) suggested that the Hebrides may have been a source of immigration into Orkney in recent years. There are currently 21 breeding patches in Orkney. This has increased from 15 in 1960 when the annual grey seal surveys began. Generally the areas colonised by seals on Orkney are sandy beaches or rocky geos. There are few steep cliffs at these sites, so the breeding seals have spread onto the grassy inland areas of a number of patches.

In this chapter, I will quantify the characteristics of habitat occupied by breeding grey seals on a range of patches in Orkney, and compare these with the characteristics of the habitats used by grey seals on the Isle of May. This will determine whether or not it is possible to develop a general model for predicting future habitat use by breeding grey seals.

4.2 Methods

Study sites:

The grey seal breeding colonies in Orkney, Scotland (Figure 4.2.1) are ideal sites at which to study grey seal colony expansion and development. The colonies in Orkney have shown the biggest increase in pup production of any UK colonies in recent years and it is of interest to see in which areas there remains the potential for further increase. Also, very few detailed field studies of breeding grey seals have been carried out in Orkney.

Three grey seal breeding patches in Orkney were selected to examine the effects of topography on the distribution of pups and the spread of pups over time (Figure 4.2.1). Ruskholm (59°12'N, 2°50'W) is a small, flat island (c.0.5 x 0.25km) where annual pup production has been between 200 and 300 pups for the last 20 years, therefore it is assumed this patch has reached a state of equilibrium. Cornholm (58°54'N, 2°42'W) and Copinsay (58°55'N, 2°40'W) have been regarded as a single breeding patch by SMRU for the purpose of annual aerial surveys. However, the two islands, which are connected by a sand bar at low tide, are very different topographically and probably constitute separate breeding patches (MacInnes, 2000). Cornholm is a small, flat island (c.0.6 x 0.2km) with many inland pools and large areas of low, grassy vegetation. Copinsay (c1.5 x 0.6km), has large areas of beach, many of which are backed by impenetrable cliffs. Much of the vegetated area of the island is very steep, or is fenced farmland. Both patches have only been surveyed by SMRU since 1993. Small numbers of pups have probably been born on Copinsay for many years,

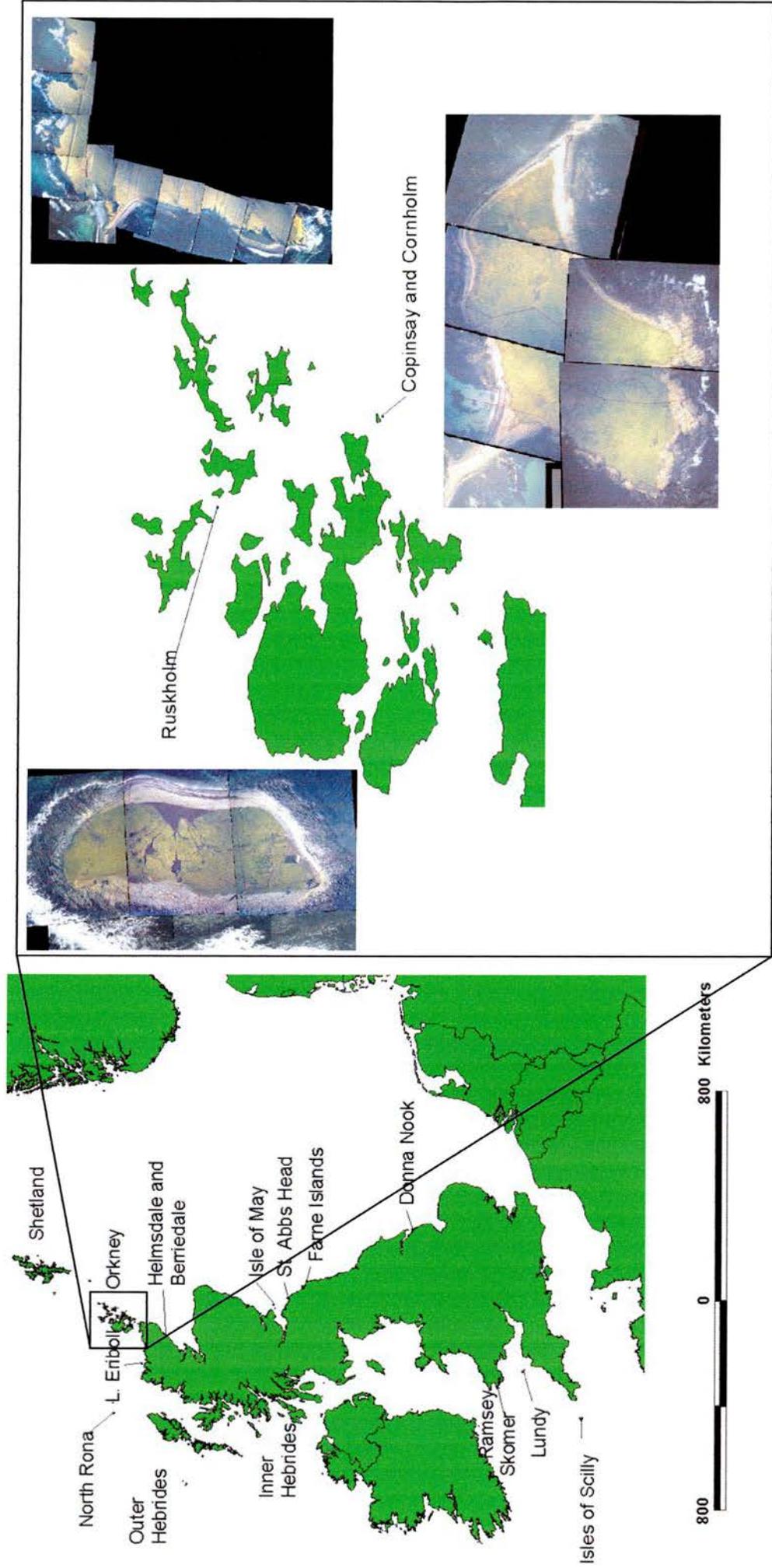


Figure 4.2.1: Grey seal breeding patches around the UK and the three study patches in Orkney.

but Cornholm was definitely not colonised until the early 1990s. Combined pup production for both patches has increased from 514 in 1993 to 2540 in 2001.

To compare the spread of pups within a season on each island, three aerial survey dates were chosen for each island to represent early, middle and late periods during the 1999 breeding season. In addition, three survey dates from 1993 for Cornholm were used to examine inter-seasonal differences between early and later phases of colonisation.

Extraction of data from aerial photographs:

The relevant aerial survey photographs were digitised, rectified to real world coordinates and tessellated in the manner described in Chapter 3 so that topographical and pup distribution data could be extracted. Traditionally, grey seal pups have been divided into five developmental stages (Boyd *et al.*, 1962), stage 1 to 3 pups have white natal coats, during stage 4 pups have started to moult and by stage 5 they are fully moulted and are generally weaned. Only the locations of stage 1 to 3 pups (white-coats) were extracted from the photographs because stage 4 and 5 pups move around so much that their positions on the patch do not necessarily represent where they were born. The topographical parameters thought to be influential in pupping site choice were slope, distance to an access point to the sea taking account of the costs of covering this distance, and cost distance to the nearest water source (inland pools or the sea). These three parameters were derived from Ordnance Survey Land-Form Panorama Digital Elevation Models and vector layers extracted from the scanned images using the method described in Chapter 3 and Twiss *et al.* (2000a).

Topographical and pup presence/absence surfaces were generated at a resolution of 5m x 5m. For each island the slope and distance to access surfaces did not change over time; however distance to water surfaces differed with survey date because varying precipitation rates, both within and between seasons, affected the location and extent of inland pools of water. Once these surfaces had been created they were exported from Arcview 3.2 (ESRI) and stacked into columns in R1.3.0.

Testing for topographical differences between occupied and unoccupied cells:

The data from each survey were divided into those cells that were occupied by white-coated pups and those that were unoccupied. For each survey date on each island a Mann-Whitney U test was used to compare the distributions of the three topographical parameters between occupied and unoccupied cells (Twiss *et al.*, 2001).

Testing for topographical differences between years, islands and survey dates for occupied cells:

To test for differences in inter-season, inter-island, intra-season and intra-island pup distributions with respect to topography, it was necessary to take account of the amount of each habitat type that was available. The topographical parameter values for all occupied cells were binned into habitat categories, and cells within each category were sampled without replacement to create a new data set with an equal number of observations in each category. Distance to access values were divided into 10m bins up to 100m, with a single bin for all cells over 100m from

an access point. Distance to water values were divided into 10m bins up to 50m, with a single bin for all cells over 50m from a water source. Only Ruskholm and Copinsay were included in the comparison of slope values because the slope values on Cornholm only ranged between 0-2°. As a result, no inter-season comparison was made of the distribution of pups in relation to slope. Slope values for Ruskholm and Copinsay were divided into two bins: less than and greater than 10°. For each parameter, nested Analyses of Variance were performed on the values for occupied cells in the sub-sampled data sets.

As the distance to access to the sea of occupied cells is unlikely to be independent from the availability of inland pools of water, the data were re-sampled taking the availability of water into account. The habitat categories were redefined using a contingency table of distance to access and distance to water. As before, the sample size used for sub-sampling was the number of cells in the habitat bin with the least number of cells. Random samples were obtained from each category for the two topographical characteristics and nested Analyses of Variance were performed on the re-sampled data sets.

4.3 Results

The distributions of white-coated pups and pools for the twelve survey dates are shown in Figure 4.3.1.

Comparison of occupied and unoccupied cells:

Cornholm

For each of the three survey dates on Cornholm in 1993 occupied cells had significantly lower mean ranks than unoccupied cells for all three topographical parameters (Table 4.3.1). In 1999 occupied cells had significantly lower mean ranks than unoccupied cells for all three topographical parameters with the exception of slope values on the 16 October 1999 and distance to water values on the 29 November 1999 (Table 4.3.2).

Ruskholm

On Ruskholm, there was no significant difference in the mean ranks of slope values between occupied and unoccupied cells. However, occupied cells had significantly lower mean ranks than unoccupied cells for distance to access and distance to water values on all dates (Table 4.3.3).

Copinsay

On Copinsay in 1999 occupied cells had lower mean ranks than unoccupied cells for distance to access, distance to water and slope on all dates (Table 4.3.4).

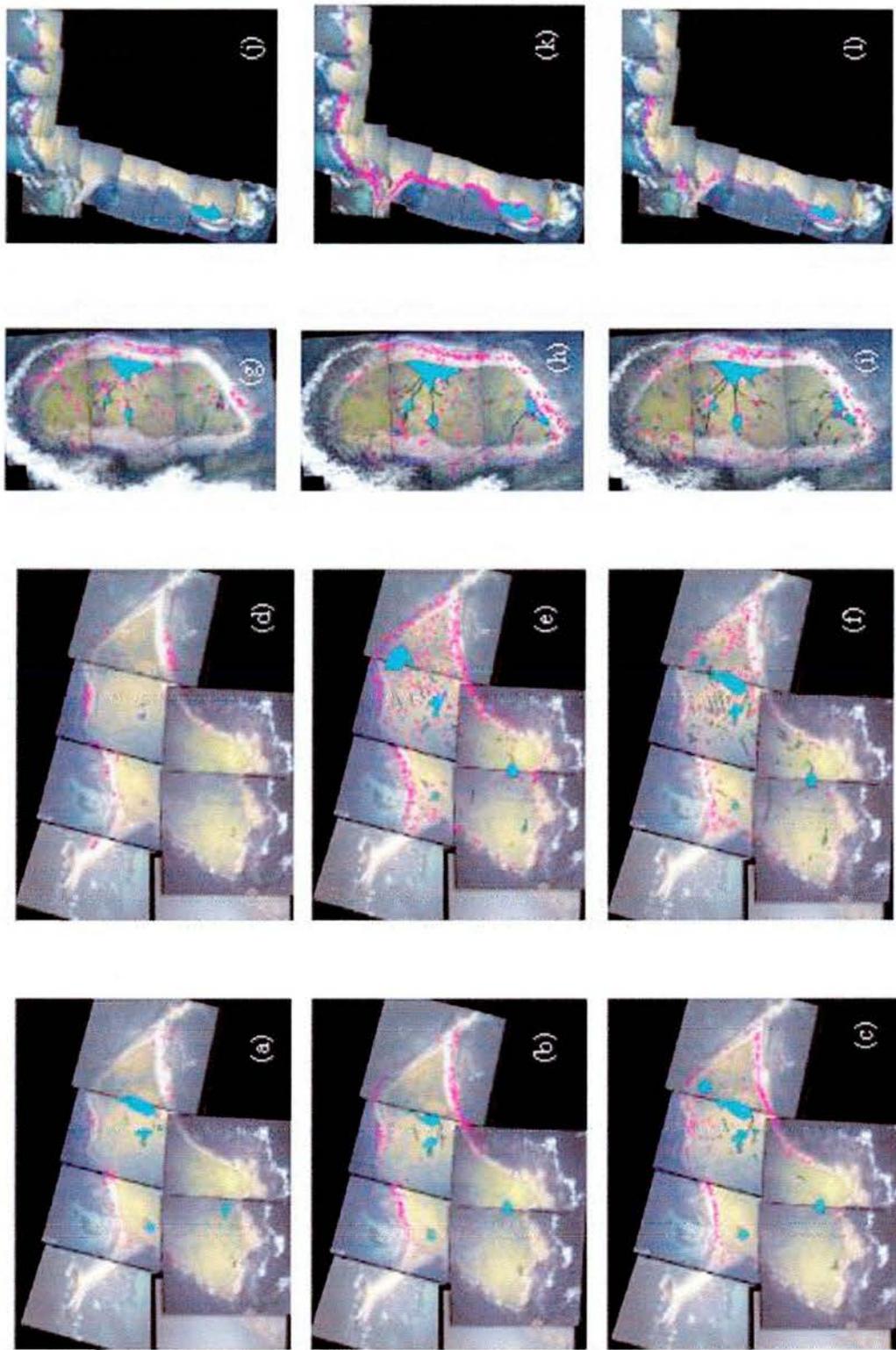


Figure 4.3.1: Positions of white-coated pups and pools of water on (a) Cornholm 16 October 1993, (b) Cornholm 5 November 1993, (c) Cornholm 16 November 1993, (d) Cornholm 16 October 1999, (e) Cornholm 11 November 1999, (f) Cornholm 29 November 1999, (g) Ruskholm 16 October 1999, (h) Ruskholm 11 November 1999, (i) Ruskholm 17 November 1999, (j) Copinsay 16 October 1999, (k) Copinsay 11 November 1999, (l) Copinsay 29 November 1999.

Table 4.3.1: Summary statistics and results of the Mann-Whitney U test comparing occupied and unoccupied cells on each date on Cornholm in 1993, (a) 16 October 1993, (b) 5 November 1993, (c) 16 November 1993.

(a)

Cornholm 16 October 1993		min	1 st quantile	median	mean	3 rd quantile	max	Result of Mann- Whitney
Distance to water	Cells with pups	5.00	5.52	12.07	16.80	15.00	79.51	(w=17325, n=5159, p=0.00078)
	Cells without pups	4.997	15.000	31.230	37.100	55.020	107.10	
Distance to access	Cells with pups	5.00	5.52	12.07	16.80	15.00	79.51	(W=11568, n=5278, p=9e-6)
	Cells without pups	4.998	25.000	65.030	75.500	111.10	254.20	
slope	Cells with pups	0.2164	0.2448	0.3745	0.6108	0.9157	1.4450	(w=18903, n=5278, p=0.001624)
	Cells without pups	0.3999	0.6076	0.8863	0.9548	1.2640	2.2920	

(b)

Cornholm 5 November 1993		min	1 st quantile	median	mean	3 rd quantile	max	Result of Mann- Whitney
Distance to water	Cells with pups	5.00	5.00	10.00	11.16	15.00	59.49	(w=81492.5, n=5185, p=2.2e-16)
	Cells without pups	4.998	15.000	33.280	37.810	55.000	119.000	
Distance to access	Cells with pups	5.00	5.00	10.00	11.53	15.00	95.73	(w=54957.5, n=5278, p=2.2e-16)
	Cells without pups	4.998	26.210	67.070	76.560	111.800	254.200	
slope	Cells with pups	0.03691	0.14090	0.35230	0.49710	0.82690	1.45900	(w=106917, n=5278, p=2.2e-16)
	Cells without pups	0.4048	0.6149	0.8913	0.9605	1.2690	2.2920	

(c)

Cornholm 16 November 1993		min	1 st quantile	median	mean	3 rd quantile	max	Result of Mann- Whitney
Distance to water	Cells with pups	5.00	12.07	17.07	19.10	25.00	53.28	(w=194980.5, n=5129, p=2.77e-9)
	Cells without pups	4.997	14.140	29.140	34.710	51.210	114.100	
Distance to access	Cells with pups	5.00	12.07	17.08	21.85	25.00	69.16	(w=123597.5, n=5278, p=2.2e-16)
	Cells without pups	4.998	25.620	67.100	76.530	112.000	254.200	
slope	Cells with pups	0.0000 0	0.09594	0.35590	0.46260	0.68400	2.07000	(w=109555.5, n=5278, p=2.2e-16)
	Cells without pups	0.4059	0.6172	0.8954	0.9620	1.2700	2.2920	

Table 4.3.2: Summary statistics and results of the Mann-Whitney U test comparing occupied and unoccupied cells on each date on Cornholm in 1999, (a) 16 October 1999, (b) 11 November 1999, (c) 29 November 1999.

(a)

Cornholm 16 October 1999		min	1 st quantile	median	mean	3 rd quantile	max	Result of Mann- Whitney
Distance to water	Cells with pups	5.000	5.000	7.076	13.920	12.070	107.800	(w=37307, n=5277, p=2.2e-16)
	Cells without pups	4.998	20.000	44.140	53.350	72.090	211.200	
Distance to access	Cells with pups	5.000	5.000	8.538	16.080	12.590	122.800	(w=34770.5, n=5278, p=2.2e-16)
	Cells without pups	4.998	25.000	66.220	75.890	111.200	254.200	
slope	Cells with pups	0.1709	0.4446	0.7949	0.8570	1.2370	1.8310	(w=108745, n=5278, p=0.1104)
	Cells without pups	0.4002	0.6072	0.8863	0.9547	1.2650	2.2920	

(b)

Cornholm 11 November 1999		min	1 st quantile	median	mean	3 rd quantile	max	Result of Mann- Whitney
Distance to water	Cells with pups	4.999	10.000	17.070	22.040	29.140	81.560	(w=866471, n= 5196, p=1.491e-14)
	Cells without pups	4.997	14.140	26.210	28.310	40.360	85.700	
Distance to access	Cells with pups	5.00	14.14	25.01	41.73	61.31	254.20	(w=705253, n= 5278, p=2.2e-16)
	Cells without pups	4.998	28.280	70.000	78.640	115.000	253.40 0	
slope	Cells with pups	0.0000	0.1505	0.4372	0.5647	0.8800	2.2520	(w=548832, n=5278, p=2.2e-16)
	Cells without pups	0.4284	0.6441	0.9197	0.9803	1.2840	2.2920	

(c)

Cornholm 29 November 1999		min	1 st quantile	median	mean	3 rd quantile	max	Result of Mann- Whitney
Distance to water	Cells with pups	4.998	10.000	17.070	21.430	28.280	73.280	(w=487439.5, n=5097, p=0.2622)
	Cells without pups	4.997	10.000	20.000	22.500	31.230	72.420	
Distance to access	Cells with pups	5.00	19.14	44.57	55.83	73.94	254.20	(w=430194, n=5278, p=2.458e-6)
	Cells without pups	4.998	25.000	67.070	76.150	112.000	253.40	
slope	Cells with pups	0.0000	0.1966	0.5091	0. 5801	0.8188	2.0390	(w=270633.5, n=5278, p=2.2e-16)
	Cells without pups	0.4089	0.6218	0.9014	0.9654	1.2730	2.2920	

Table 4.3.3: Summary statistics and results of the Mann-Whitney U test comparing occupied and unoccupied cells on each date on Ruskholm in 1999, (a) 16 October 1999, (b) 11 November 1999, (c) 17 November 1999.

(a)

Ruskholm 16 October 1999		min	1 st quantile	median	mean	3 rd quantile	max	Result of Mann- Whitney
Distance to water	Cells with pups	4.906	5.000	7.415	14.860	20.000	54.790	(w=42559.5, n=3719, p=1.538e-6)
	Cells without pups	4.906	12.070	22.070	24.440	33.630	75.000	
Distance to access	Cells with pups	5.00	5.00	10.00	22.03	30.29	90.58	(w=34359, n=3846, p=6.737e-10)
	Cells without pups	5.00	22.36	45.65	49.95	75.29	120.90	
slope	Cells with pups	0.000	0.000	0.000	1.531	0.000	15.620	(w=76707, n=3846, p=0.76)
	Cells without pups	0.000	0.000	0.000	1.808	0.000	15.620	

(b)

Ruskholm 11 November 1999		min	1 st quantile	median	mean	3 rd quantile	max	Result of Mann- Whitney
Distance to water	Cells with pups	5.00	5.00	10.00	16.11	20.00	74.28	(w=131467.5 , n=3653, p=1.469e-14)
	Cells without pups	4.906	12.070	24.140	27.220	39.140	81.290	
Distance to access	Cells with pups	5.000	7.071	19.140	31.820	50.290	118.00	(w=149593, n=3846, p=3.531e-13)
	Cells without pups	5.00	24.43	46.80	50.28	75.29	120.90	
slope	Cells with pups	0.0000	0.0000	0.0000	0.8071	0.0000	14.850	(w=220740, n=3846, p=0.01056)
	Cells without pups	0.00	0.00	0.00	1.84	0.00	15.62	

(c)

Ruskholm 17 November 1999		min	1 st quantile	median	mean	3 rd quantile	max	Result of Mann- Whitney
Distance to water	Cells with pups	5.00	5.00	12.07	14.68	19.58	47.77	(w=106753, n=3665, p=2.346e-7)
	Cells without pups	4.906	10.290	19.140	21.240	29.140	66.510	
Distance to access	Cells with pups	5.000	7.329	18.400	33.660	49.540	117.50	(w=108653, n=3846, p=3.643e-8)
	Cells without pups	5.00	24.14	45.82	50.03	75.29	120.90	
slope	Cells with pups	0.000	0.000	0.000	1.816	0.000	15.620	(w=165200.5 , n=3846, p=0.9805)
	Cells without pups	0.000	0.000	0.000	1.805	0.000	15.620	

Table 4.3.4: Summary statistics and results of the Mann-Whitney U test comparing occupied and unoccupied cells on each date on Copinsay in 1999, (a) 16 October 1999, (b) 11 November 1999, (c) 29 November 1999.

(a)

Copinsay 16 October 1999		min	1 st quantile	median	mean	3 rd quantile	max	Results of Mann-Whitney
Distance to water	Cells with pups	4.647	5.00	5.760	6.623	6.228	13.79	(w=7532, n=24390, p=5.912e-10)
	Cells without pups	4.292	108.10	222.500	240.9	361.400	684.600	
Distance to access	Cells with pups	4.647	5.00	5.760	6.623	6.228	13.79	(w=6663, n=24572, p=4.735e-10)
	Cells without pups	4.292	113.300	227.600	243.8	360.300	384.600	
Slope	Cells with pups	4.520	6.212	17.780	15.21	21.840	26.570	(w=629083, n=27724, p=0.006251)
	Cells without pups	2.025	5.711	7.265	12.21	12.760	53.400	

(b)

Copinsay 11 November 1999		min	1 st quantile	median	mean	3 rd quantile	max	Result of Mann-Whitney
Distance to water	Cells with pups	4.906	7.071	12.070	15.530	19.490	70.330	(w=408270, n=24294, p=2.2e-16)
	Cells without pups	4.292	110.000	220.900	240.10	359.200	684.600	
Distance to access	Cells with pups	5.000	7.415	14.140	19.570	24.920	92.060	(w=422461.5, n=24572, p=2.2e-16)
	Cells without pups	4.292	118.700	231.500	247.40	362.600	684.600	
slope	Cells with pups	0.000	5.711	6.379	7.840	10.220	29.500	(w=3159193, n=3846, p=2.2e-16)
	Cells without pups	4.520	6.379	8.294	13.410	15.790	53.400	

(c)

Copinsay 29 November 1999		min	1 st quantile	median	mean	3 rd quantile	max	Result of Mann-Whitney
Distance to water	Cells with pups	4.906	10.290	17.360	22.170	27.990	83.210	(w=212459.5, n=24369, p=2.2e-16)
	Cells without pups	4.292	106.700	218.60	237.90	357.700	684.600	
Distance to access	Cells with pups	5.00	13.72	19.83	26.74	33.95	83.21	(w=217892.5, n=24572, p=2.2e-16)
	Cells without pups	4.292	114.800	228.60	244.90	361.100	684.600	
slope	Cells with pups	2.025	5.711	6.217	7.709	10.020	21.960	(w=1440217, n=27724, p=7.095e-07)
	Cells without pups	2.025	5.711	7.265	12.240	13.340	53.400	

Among year, islands and survey date comparisons for occupied cells:

When data from all occupied cells were analysed, mean distance to access differed significantly between years, among islands, among islands within years, among survey dates, and among dates within years and dates within islands (Table 4.3.5). The mean distance to water of occupied cells for Cornholm in 1999 was not significantly different from the mean distance observed in 1993 (Table 4.3.6). There was a significant difference in mean distance to water among islands but not among survey dates within each island, as a result there was no significant increase or decrease in distance to water as the season progressed (Table 4.3.6). The mean slope value did not differ significantly among islands or among survey dates (Table 4.3.7).

When the availability of each habitat category was taken into account, there were still significant differences among seasons, islands and survey dates for distance to access (Table 4.3.8). However, differences among islands for distance to water were no longer significant (Table 4.3.9).

The mean distance to access of cells occupied by pups differed among islands, even when the number of pups on each island and the availability of water were both taken into account (Table 4.3.10). When pup numbers on all three islands were relatively low, the mean distance to access on Ruskholm was greater than on Cornholm and Copinsay. When there were high pup numbers present on Copinsay and Cornholm the mean distance to access was greatest on Cornholm.

Table 4.3.5: Comparison of mean distance to access between seasons, islands and dates, and within islands.

	DF	F value	Pr(>F) * 0.05 **0.01 ***0.001
Season	1	26.5082	***
Island	2	28.4288	***
Date	1	32.9723	***
Date within Island	1	44.7299	***

Table 4.3.6: Comparison of mean distance to water between seasons, islands and dates, and within islands.

	DF	F value	Pr(>F) * 0.05 **0.01 ***0.001
Season	1	0.8733	
Island	2	7.6397	***
Date	1	0.6175	
Date within Island	1	1.3422	

Table 4.3.7: Comparison of mean slope between islands and dates.

	DF	F value	Pr(>F) * 0.05 **0.01 ***0.001
Island	1	3.5491	
Date	1	0.1364	

Table 4.3.8: Comparison of mean distance to access between seasons, islands and dates, within seasons and within islands taking water availability into account.

	DF	F value	Pr(>F) * 0.05 **0.01 ***0.001
Season	1	4.5124	*
Island	2	9.3358	***
Date	1	5.7416	*
Date within Island	1	7.6085	**

Table 4.3.9: Comparison of mean distance to water between seasons, islands and dates, within seasons and within islands taking access availability into account.

	DF	F value	Pr(>F) * 0.05 **0.01 ***0.001
Season	1	1.8723	
Island	2	2.1682	
Date	1	0.0356	
Date within Island	1	0.0013	

Table 4.3.10: Comparison of mean distance to access of occupied cells across islands in instances when the same numbers of pups were present on both patches.

Island and Date	Number of pups present	Number of occupied cells	Mean distance to access (m)
Cornholm 16 October 1999	98	82	28.6
Ruskholm 17 November 1999	110	106	57.9
Cornholm 16 November 1993	157	129	15.5
Ruskholm 11 November 1999	159	142	23.9
Copinsay 29 November 1999	163	157	17.7
Cornholm 11 November 1999	620	524	40.1
Copinsay 11 November 1999	613	447	17.0

4.4 Discussion

Twiss *et al.* (2001) showed that cells occupied by breeding grey seals on two patches on the Isle of May in 1994 were significantly closer to access to the sea and water than unoccupied cells. However, they found that there was no difference in the slope values of occupied and unoccupied cells. Similar patterns were found in this analysis of three breeding patches in Orkney over a number of dates and years. There was a single case (Cornholm, 29 November 1999) where there was no significant difference in the distance to water values of occupied and unoccupied cells. This was probably due to the high levels of precipitation in the days before 29 November 1999, which created large numbers of inland pools throughout the island. This greatly reduced the range of distances to water for unoccupied cells.

The slope values of occupied and unoccupied cells were significantly different on Copinsay, in contrast to the situation on the Isle of May, Cornholm and Ruskholm. The widest range of slope values was observed on the Isle of May (Twiss *et al.*, 2001) and pups were found throughout the available range. However, on Copinsay, pups were only found within the lower part of the range of available slopes. These differences are probably due to the different types of topography that are available close to the access point on each island. On Copinsay there are large areas of low-lying habitat close to the access points to the sea, whereas on the Isle of May the topography close to the access point is much more variable. However, all the low-lying habitat that is available close to

access on Copinsay has yet to be occupied, and habitats with steeper slopes may be occupied when the low-lying habitat is saturated with breeding females.

The mean distance to access to the sea of occupied cells differed among survey dates. On Cornholm, occupied cells were further from an access point in 1999 than in 1993. In 1999, occupied cells on Copinsay were closer to access points than those on Cornholm. Mean distance to access increased as the season progressed on all islands, in both 1993 and 1999. These differences in mean distance to an access point were not explained by the differing availability of inland pools of water among seasons, islands and survey dates. The observed inter- and intra-seasonal differences cannot be caused by the characteristics of the access points and must, at least partially, be caused by differences in the number of pups present. At UK colonies, older, larger females tend to give birth earlier in the season than young females (Fedak and Anderson, 1982; Pomeroy *et al.*, 1999; Twiss *et al.*, 2000a; Twiss *et al.*, 2000b). This difference in the age- and size-structure of females arriving early and late in the season, and their ability to compete for pupping sites close to an access point (Twiss *et al.*, 2000a), may account for some of the observed differences.

Controlling for the availability of habitat close to an access point eliminated the inter-island difference in the distance to water of occupied cells. This implies that, once differences in access type are accounted for, all females make similar decisions about where to give birth, in terms of slope and proximity to water.

The quantification of the relationship between the distribution of a species and its habitat is one of the most important aspects of predictive modelling in ecology (Guisan and Zimmermann, 2000). The consistent relationship between the locations of pups and distance to the closest water source and slope values of occupied cells across patches observed in this study provides the basis for a general predictive model of the distribution of grey seals on individual breeding patches.

Chapter 5

The Influence of Aggression and Topography on the Distribution of Breeding Grey Seals.

5.1 Introduction

The need to identify suitable habitat for a species has become more pressing as the conservation status of many species has become more acute. One of the most important research areas in ecology is concerned with determining the environmental factors that influence a species' distribution (Manel *et al.*, 2001). Studying and quantifying a species' current habitat usage can provide information on its biological requirements (Arthur *et al.*, 1996). The grey seal (*Halichoerus grypus*) is listed as a "Species of Community Interest" under the European Directive on Species and Habitats (Council Directive 92/43/EEC), which requires Member States of the European Union to identify Special Areas for Conservation (SACs) for this species. In the UK, candidate sites for SACs have been identified using estimates of annual pup production provided by the Sea Mammal Research Unit (Anon., 1997). Once an SAC has been established, it must be managed to ensure that the conservation status of the protected species remains favourable (i.e. that "there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis"). Harwood and Prime (1978) suggested that the ultimate determinant of the size of a local grey seal population, defined as "the set of individuals which all interact with each other with a high probability" (Gilpin and Hanski, 1991), is determined by the number of potential pupping sites within the patch occupied by that population. Therefore, identifying the characteristics of suitable pupping sites will make it possible to predict how far populations in SACs

are likely to spread within their patches, and to identify patches that are currently unoccupied.

A small number of the grey seal breeding colonies around the UK have been intensively studied and there are numerous qualitative descriptions of the factors that appear to be used by females when selecting a pupping site (Anderson and Harwood, 1985; Boyd *et al.*, 1962; Caudron, 1995; Pomeroy *et al.*, 1994; Pomeroy *et al.*, 2000a; Prime, 1981). The possible topographical factors involved in pupping site choice have been quantified on an individual scale at two breeding patches on the Isle of May (Scotland) and one breeding patch on North Rona (Scotland) (Twiss *et al.*, 2000a; Twiss *et al.*, 2001). These colonies have been studied extensively over a number of years. Pup production at North Rona has been relatively stable for many years, so the distribution of pupping sites in relation to habitat availability may differ from that in newly colonised patches, such as the Isle of May.

The dynamic response of a species to environmental change has rarely been studied in detail (Guisan and Zimmermann, 2000). For most species the most common environmental change is likely to be associated with large-scale changes in land use or climate change. However for the purposes of this study, I will use the term environmental change to refer to the fine-scale spatio-temporal changes on a breeding patch that occur within a breeding season. Previous studies on grey seal habitat preferences have not taken into account the changes in habitat characteristics that occur within a breeding season.

The grey seal breeding season lasts about 7-8 weeks, but an individual female only stays ashore for 18-20 days during which time she gives birth, raises her pup and mates. There is, therefore, a turnover of females during the course of a breeding season. This means that, in order to estimate total pup production in a patch, four or five aerial surveys must be carried out in each breeding season because no individual survey will include all the pups born (Harwood, 1997; Ward, 1987). The series of aerial surveys can be used to estimate a number of parameters associated with the breeding process, and the distribution of pups in each survey can be used to test the predictions of mathematical models of the way in which females chose their pupping sites. Not only can some of the topographical characteristics of a patch change over the course of the breeding season, a female's choice of pupping site is also likely to be based on the distribution of other females at the time she comes ashore. This will change on a daily basis as new females arrive and others leave.

Most females arrive at a patch at least 2-3 days before giving birth (Burton *et al.*, 1975; Pomeroy *et al.*, 1994; Pomeroy *et al.*, 2000a). Disturbance during this period may cause a female to look elsewhere for a suitable site. As grey seals tend to aggregate (Boness and James, 1979), the sites chosen by the first animals that come ashore may influence the distribution of later individuals. At a fine enough scale (approximately equal to the size of a seal) the presence of another individual will prevent a female from choosing a particular site because it is already occupied.

Many behavioural studies of breeding patches have observed responses by breeding females to conspecifics that could regulate the density within a patch (Anderson *et al.*, 1975; Boness *et al.*, 1982; Caudron, 1998; Harcourt, 1991; Kovacs, 1987; Pomeroy *et al.*, 2000a). 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 become intolerant of conspecifics and intruders once they have given birth (Boness *et al.*, 1982; Harcourt, 1990; Pomeroy *et al.*, 2000a). This intolerance often leads to aggressive interactions between individuals. Such aggression 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). Caudron (1998) found that, on the Isle of May, conspecifics were threatened by mothers with pups if they approached within two body lengths. The median nearest neighbour distance between adult females in this patch was 2.3-3.4m, this corresponds to a local density of approximately one adult per 10m². This probably sets an upper limit to the degree of aggregation that will be tolerated within a patch. However, levels of aggression at different locations within a breeding patch cannot be measured from the aerial photographs, so this factor cannot be incorporated explicitly into a model of habitat suitability and some measurable proxy must be identified.

An observational field study was carried out on the Isle of May, Scotland to determine the way in which levels of aggression varied with location and pup presence over time. The probability of an aggressive encounter on a particular day

was related to topography, pup presence and habitat type. This relationship was used to predict where newborn pups were most likely to be born on each day. The original scale of the model was set at 2m x 2m, to ensure that no more than one animal could ever be recorded in a cell.

Presence/absence data of this kind are often analysed using generalised linear models - GLMs (Augustin *et al.*, 1996; Buckland and Elston, 1993; Guisan and Zimmermann, 2000). GLMs were used in this study but, because the aim was to develop a model that was generally applicable, variables within the GLM were generalised by placing the cells into habitat categories rather than conducting the analysis on a cell-by-cell basis.

5.2 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 (Figure 5.2.1). Until the 1970's very few pups were born on the island but pup production has increased markedly and in 2001 had risen to 1932 (SCOS, 2002).

Behavioural observations were carried out on a discrete breeding patch in a gully, Kaimes, on the east side of the island where pup production was approximately 70 pups in 2000. Observations were carried out on almost all days between 29 October and 30 November 2000. On average six hours a day were spent in a hide overlooking the breeding patch. Only those days for which there was exactly six hours of observation time were included in the analysis. 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. Throughout the observation period the time and position of all aggressive interactions were recorded. On return from fieldwork the daily maps were entered into ArcView 3.2 GIS software.

Modelling presence/absence of aggressive encounters:

The location of each observed aggressive interaction was entered into a 2m x 2m presence/absence grid. The following explanatory variables, all of which can

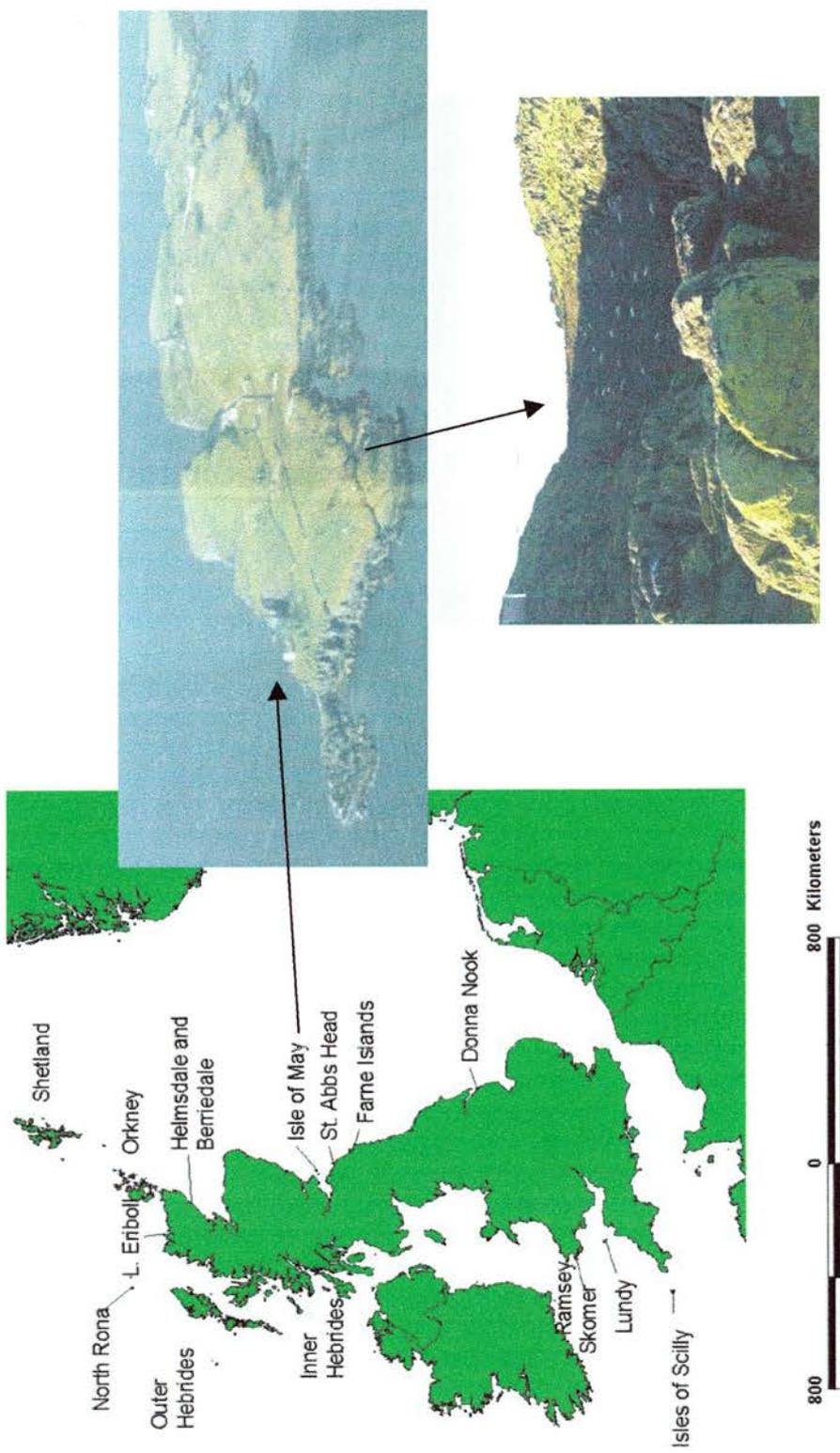


Figure 5.2.1: Location of major British grey seal breeding sites with inset of the Isle of May and the study site, Kaimes.

potentially be extracted from aerial photographs or existing datasets, were used: An Ordnance Survey Land-Form Profile Digital Elevation Model (DEM) was used to interpolate a 2m x 2m resolution height and slope surface for the study site. The distance of every cell from access to the sea and from water on each day was calculated using the Pathdistance function of Arcinfo, taking account of the elevation and slope of each cell (Chapter 3 methods, Twiss *et al*, 2000a, Appendix 3).

Grey seal pups in the study area were classified into one of the five developmental stages identified by Boyd, Lockie *et al.* (1962): stage 1 to 3 pups have white natal coats, during stage 4 the pup starts to moult and by stage 5 they are fully moulted and are generally weaned. The locations of all pups in stages 1 to 3 were converted into a 2m x 2m presence/absence grid. Stage 4 and 5 pups were not included in the analysis because they frequently change their positions within a patch and their locations do not reflect where they were born.

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

Each surface was exported from Arcview 3.2 and stacked into a column in R1.3.0. A table of surfaces was created for each day of observation in which each row in the table corresponded to a cell in the grid. All the observation days were stacked

together into one table and each row (cell) was binned into a habitat category. For the purposes of the aggression model, the habitat categories were defined by their distance from access to the sea (in 10m increments), distance to water (10m increments), slope (10 degree increments), mean number of neighbouring pups (0.1 increments), pup presence (0 or 1) and day. These habitat types were used as the explanatory variables whilst the response variable was the calculated proportion of cells in each habitat type in which aggressive encounters were observed. A generalised linear model was fitted to the data with a binomial error distribution and a probit link function. The model was weighted by the number of cells in each habitat type. Second, third and fourth order polynomial terms for day were included in the model to account for variation over time. All first and second order interaction terms were included in the model and an appropriate model was chosen using backward stepwise selection. The goodness of fit of the model was determined by the value of the scaled deviance. The scaled deviance should be distributed approximately as a chi-squared distribution with $(n-p)$ degrees of freedom if the model provides a good fit to the data, where p is the number of parameters in the fitted model and n is the number of parameters in the saturated model (Krzanowski, 1998). For a range of days the model was used to either fit or predict a probability of aggression for each cell on the grid. These were visually compared to the observed distributions of aggression for each day.

Modelling presence/absence of new born pups:

The predicted daily surfaces for probable levels of aggression were incorporated into a model to predict newborn pup distribution on each day. The response variable was the proportion of cells in each habitat type that contained a newborn pup. The same explanatory variables were used as before with the addition of the probability of an aggressive encounter in each cell. The aggression model was used to predict cell-by-cell values of aggression for each day. Therefore the habitat types were redefined with aggression probabilities included (0.25 increments). The habitat types from one day were fitted to the newborn pup positions on the following day as grey seal mothers tend to investigate suitable sites up to a few days before giving birth (Burton *et al.*, 1975). Thus, the birth position is likely to be influenced by conditions on the previous day. Due to underdispersion, a quasibinomial GLM was fitted with a probit link function. The model was weighted by the number of cells present in each habitat type. Again, up to fourth order polynomial terms for day and all first and second order interaction terms were included and backward stepwise selection was performed. Deviance cannot be used to test the goodness of fit of a quasibinomial GLM because the deviance parameter is unknown, therefore fitted versus observed plots and residual plots were examined. All days for which data were available were included in the model, not just those with six hours of observation.

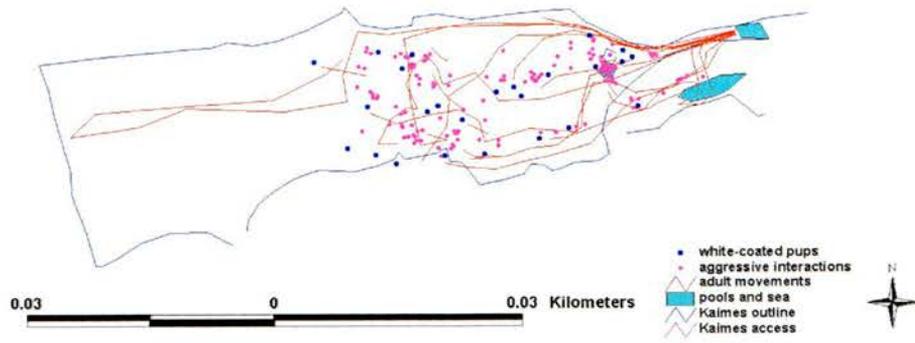
5.3 Results

The positions of white-coated pups spread inland over time as numbers increased (Figure 5.3.1). However, as pups progressed to developmental stages 4 and 5 and subsequently departed, space became available near the access point later on in the season (Figure 5.3.1c).

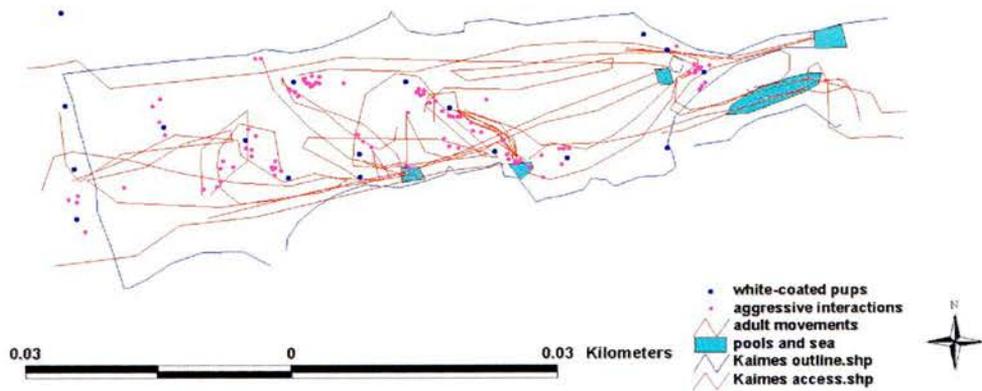
The four topographical surfaces (Figure 5.3.2a-d) show that the access gully to the sea was narrow and surrounded by steep sloping cliffs (Figure 5.3.2d). The main part of the gully, where the majority of the seals were found, was relatively flat and low-lying, with a number of freshwater pools. The maximum distance to water from any cell within the study site was 75m (Figure 5.3.2c), whereas the maximum distance to the sea was 110m (Figure 5.3.2b). The distance to water from each cell varied from day to day because of the effects of precipitation.

Model fitted to presence/absence of aggressive encounters (see Appendix 3):

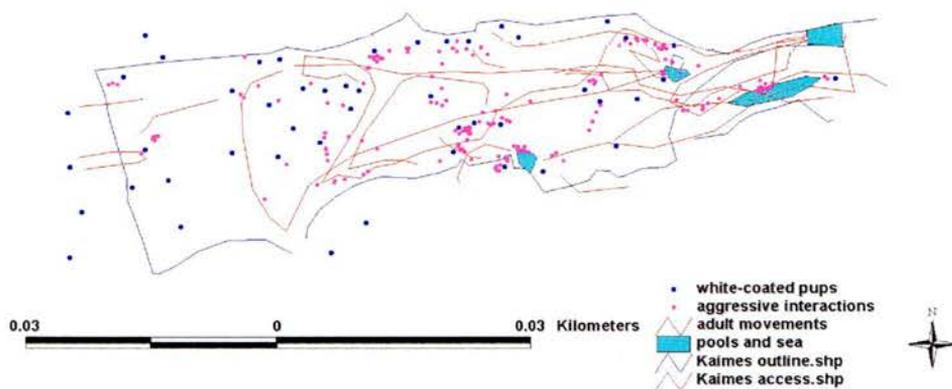
The cells for all days combined were binned into 2166 habitat categories. The categorised variables making up the habitat types for the aggression presence/absence model were plotted against the proportion of cells in each habitat type where aggressive interactions were observed (Figure 5.3.3). Aggressive encounters were predominantly observed in cells with a slope of 25° or less, and that were near to water. Aggression was seldom observed in cells where there were pups, but was more often observed in cells whose neighbouring cells contained a pup.



(a)



(b)

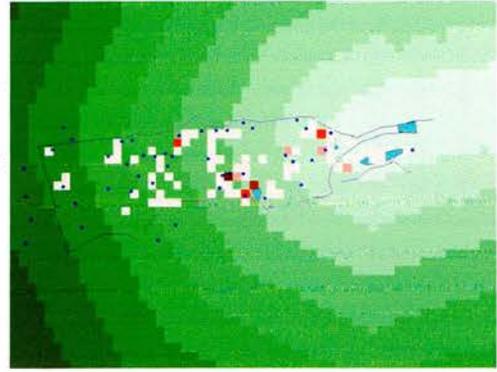


(c)

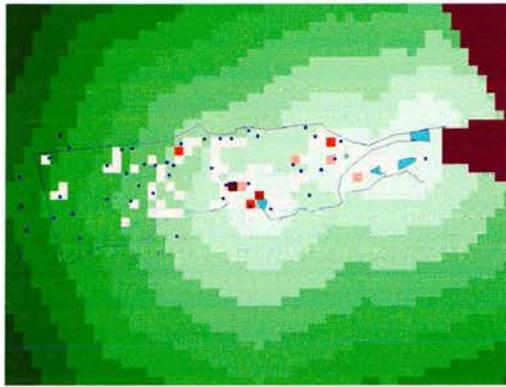
Figure 5.3.1: The white-coated pup distributions, pool positions, aggressive encounter positions and adult movements for Kaimes on (a) 31 October 2000, (b) 13 November 2000 and (c) 27 November 2000.



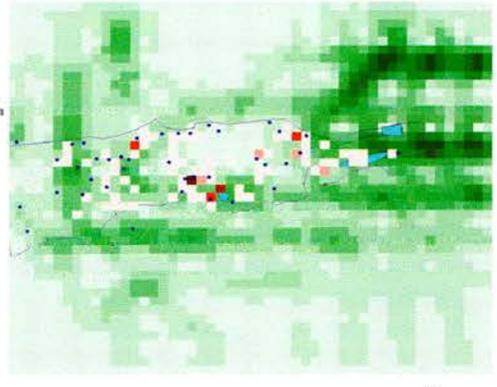
(a)



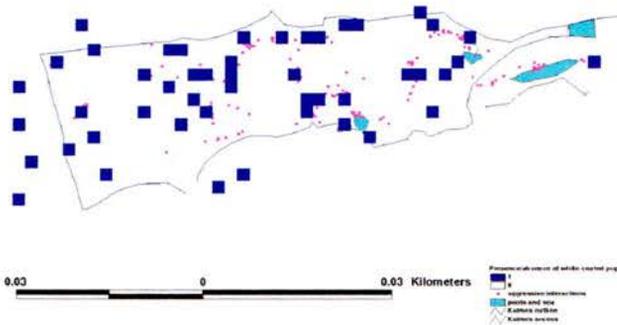
(b)



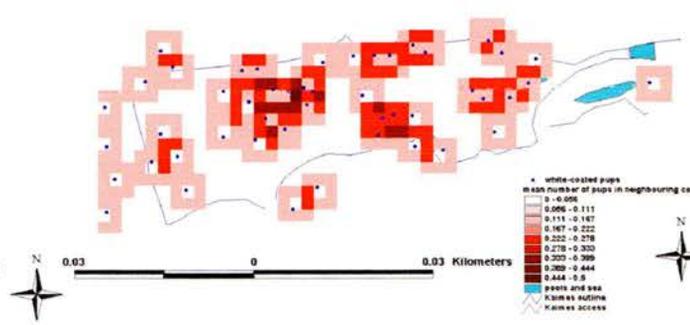
(c)



(d)



(e)



(f)

Figure 5.3.2: The habitat variables, (a) height, (b) distance to access, (c) distance to water, (d) slope, all overlay with the total number of aggressive encounters in each grid cell, (e) the presence/absence of white-coated pups and (f) the mean number of pups in neighbouring cells on the 13 November 2000.

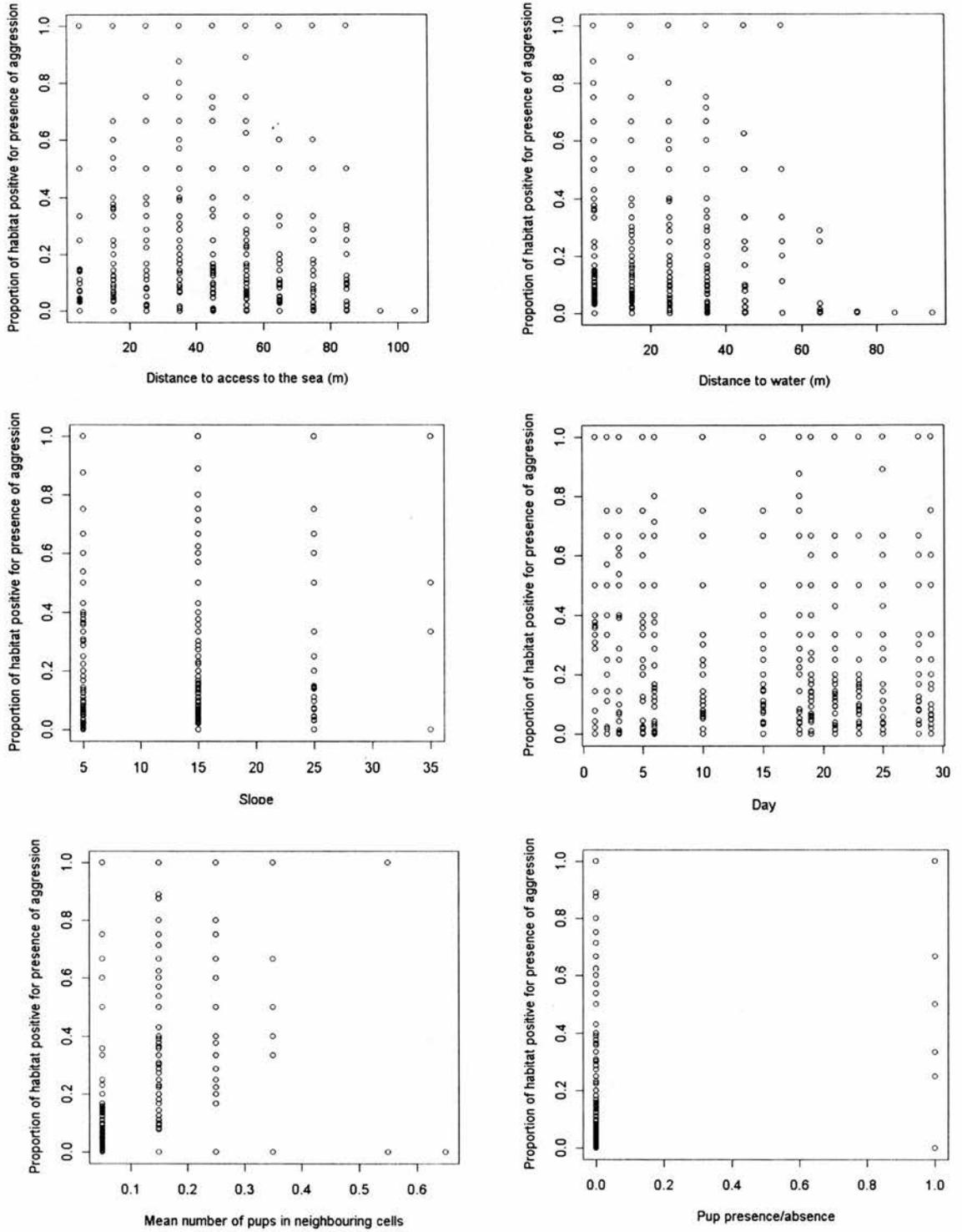


Figure 5.3.3: The proportion of each habitat type that is positive for the presence of aggressive interactions against each explanatory variable for every day of the observations on Kaimes, Isle of May, 2000.

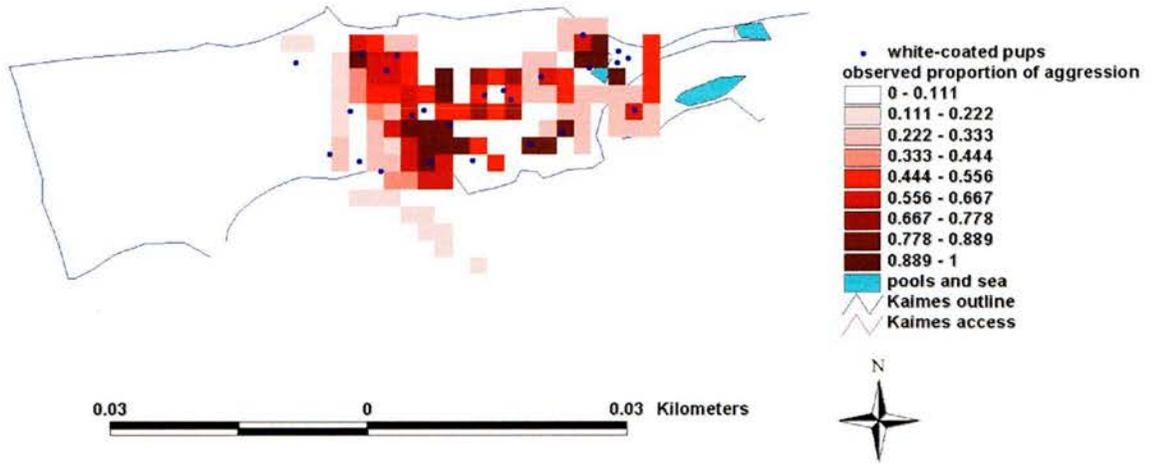
There was no clear relationship between aggression and the distance to access to the sea. The occurrence of aggression increased up to 30m from the access point and then appeared to decrease. The occurrence of aggressive interactions was fairly constant over time. The best fitting GLM retained all of the variables on their own as well as a number of polynomials and up to second order interaction terms (Table 5.3.1). In the fitted GLM, the probability of aggression decreases with increasing distance to water and day and increases with distance to access, slope, number of neighbours and pup presence.

The deviance of the fitted model was 2059.2 with 2098 degrees of freedom. $P(\chi^2_{2098} > 2059.2)$ is 0.723, so the model fit was deemed good. The fit of the model was further assessed by visual analysis of the fitted and predicted surfaces (Figures 5.3.4-5.3.8). Three dates, which were included in the model-fitting process, were chosen to represent the fit of the model at the beginning, middle and end of the observation period (Figures 5.3.4-5.3.6). On all three dates, the fitted probability of aggression was very similar to the observed aggression, although there were a few instances where the model had over-fitted the data. These mainly occurred in areas where pups were present but no aggression was observed. There were few days that were not included in the model, and only two examples of the predicted probabilities of aggression - one near the beginning and one near the end of the observation period (Figures 5.3.7-5.3.8) – have been shown. The distribution of the predicted probabilities on both dates was similar to the observed proportions of aggression. Most of the instances of over-prediction are for cells in which pups were present.

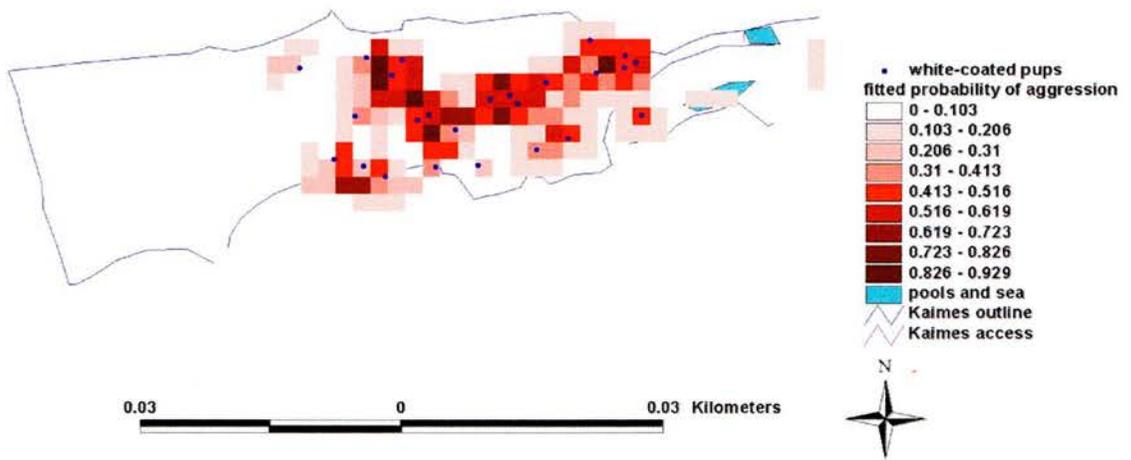
Table 5.3.1: The significance of the variables included in the GLM fitted to the daily occurrence of aggression. The significance of all individual variables is shown but only significant interaction terms have been included.

Explanatory variable	Significance * 0.05 ** 0.01 ***0	Explanatory variable	Significance * 0.05 ** 0.01 ***0
Distance to water (m)	***	Distance to water:Distance to access:Day	*
Distance to access (m)	***	Distance to water:Distance to access:Day ²	*
Slope		Distance to water:Distance to access:Day ³	**
Mean number of neighbouring pups	**	Distance to water:Distance to access:Day ⁴	*
Pup presence	**	Distance to water:Slope:Day	***
Day		Distance to water:Slope:Day ⁴	*
Day ²	*	Distance to water:Mean number of neighbouring pups:Pup presence	***
Day ³	*	Distance to water:Mean number of neighbouring pups:Day ³	.
Day ⁴	*	Distance to water:Mean number of neighbouring pups:Day ⁴	*
Distance to water:Distance to access	*		
Distance to water:Mean number of neighbouring pups	***	Distance to water:Pup presence:Day	*
Distance to water:Pup presence	***	Distance to water:Pup presence:Day ²	**
Distance to water:Day	***	Distance to water:Pup presence:Day ³	**
Distance to water:Day ²	***	Distance to water:Pup presence:Day ⁴	*
Distance to water:Day ³	***	Distance to access:Slope:Mean number of neighbouring pups	*
Distance to water:Day ⁴	***	Distance to access:Slope:Day	**
Distance to access:Slope	*	Distance to access:Slope:Day ²	*
Distance to access:Pup presence	*	Distance to access:Slope:Day ³	.
Distance to access:Day	***	Distance to access:Slope:Day ⁴	.
Distance to access:Day ²	**	Distance to access:Mean number of neighbouring pups:Pup presence	**
Distance to access:Day ³	*	Distance to access:Mean number of neighbouring pups:Day	*
Distance to access:Day ⁴	.	Distance to access:Pup presence:Day	.
Mean number of neighbouring pups:Pup presence	**	Distance to access:Pup presence:Day ²	.
Mean number of neighbouring pups:Day	**	Slope:Mean number of neighbouring pups:Day	***
Mean number of neighbouring	**	Slope:Mean number of	**

pups:Day ²		neighbouring pups:Day ²	
Mean number of neighbouring pups:Day ³	*	Slope:Pup presence:Day ²	*
Pup presence:Day ²	.	Slope:Pup presence:Day ³	*
Pup presence:Day ³	.	Slope:Pup presence:Day ⁴	*
Pup presence:Day ⁴	.	Mean number of neighbouring pups:Pup presence:Day	**
Distance to water:Distance to access:Slope	**	Mean number of neighbouring pups:Pup presence:Day	**
Distance to water:Distance to access:Mean number of neighbouring pups	***	Mean number of neighbouring pups:Pup presence:Day	**
Distance to water:Distance to access:Pup presence	**	Mean number of neighbouring pups:Pup presence:Day	*

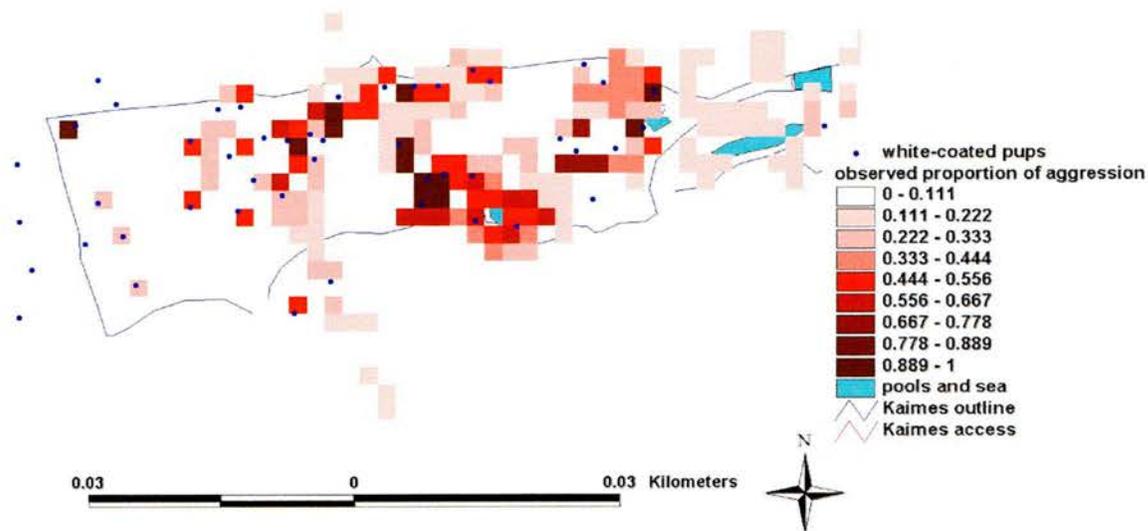


(a)

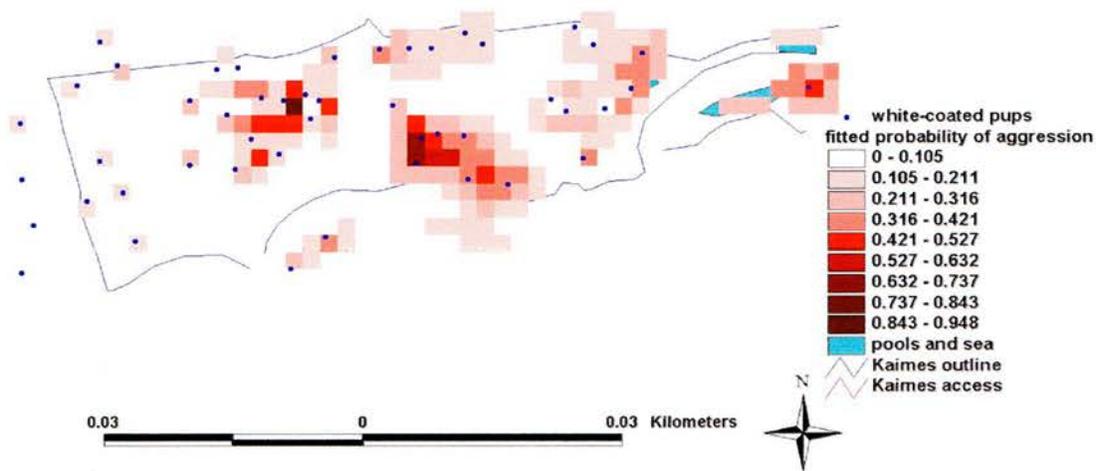


(b)

Figure 5.3.4: The observed proportions of aggression (a) and the fitted probabilities of aggression (b) occurring on the 31 October 2000 for each cell given its habitat type.

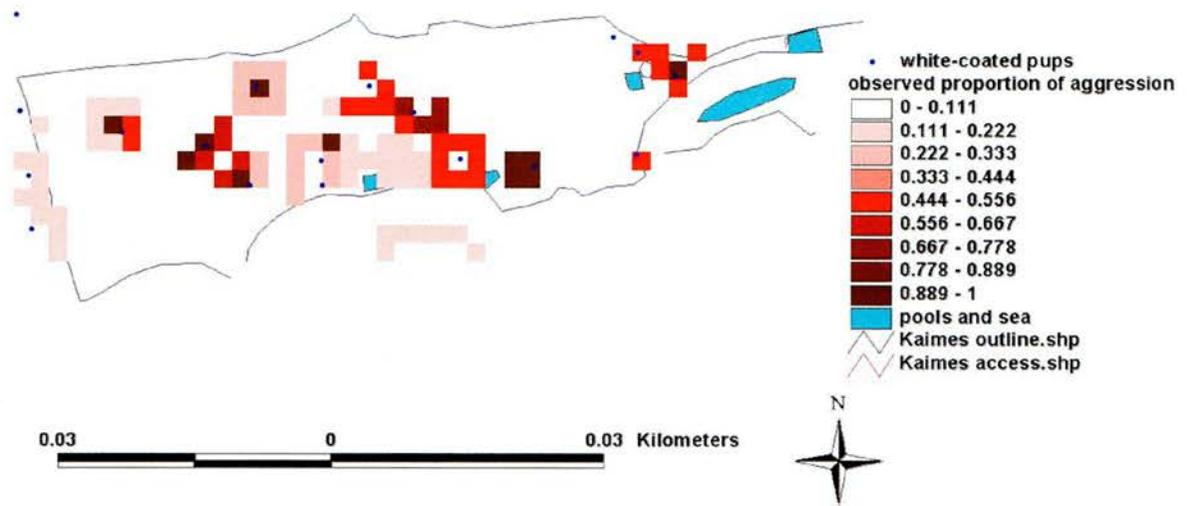


(a)

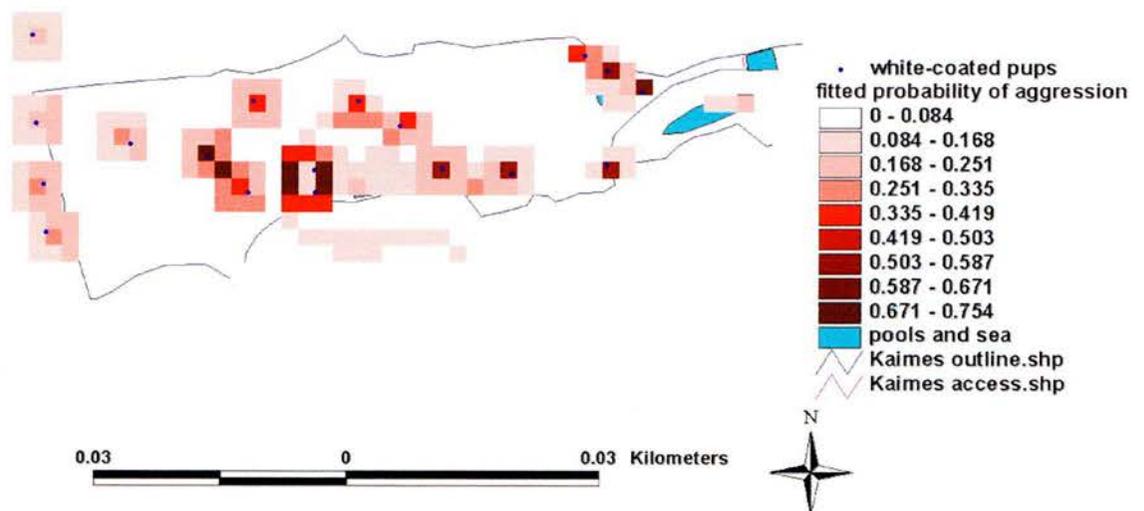


(b)

Figure 5.3.5: The observed proportions of aggression (a) and the fitted probabilities of aggression (b) occurring on the 13 November 2000 for each cell given its habitat type.

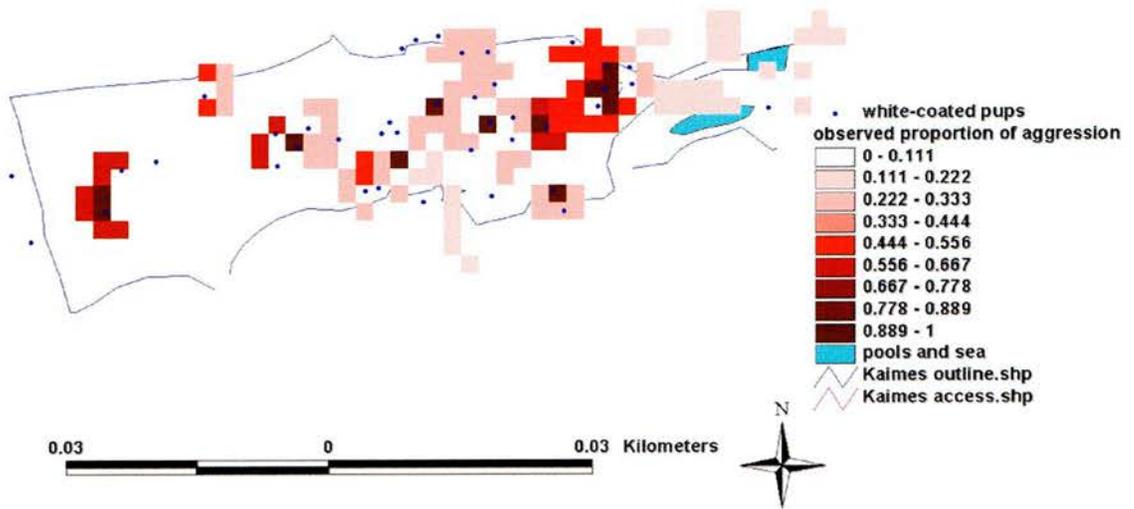


(a)

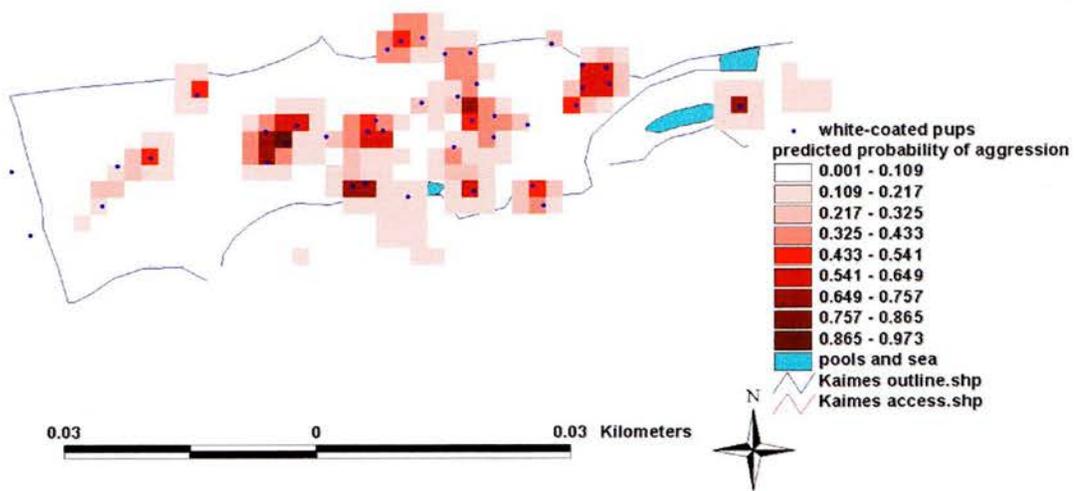


(b)

Figure 5.3.6: The observed proportions of aggression (a) and the fitted probabilities of aggression (b) occurring on the 27 November 2000 for each cell given its habitat type.



(a)



(b)

Figure 5.3.7: The observed proportions of aggression (a) and the predicted probabilities of aggression (b) occurring on the 5 November for each cell given its habitat type.

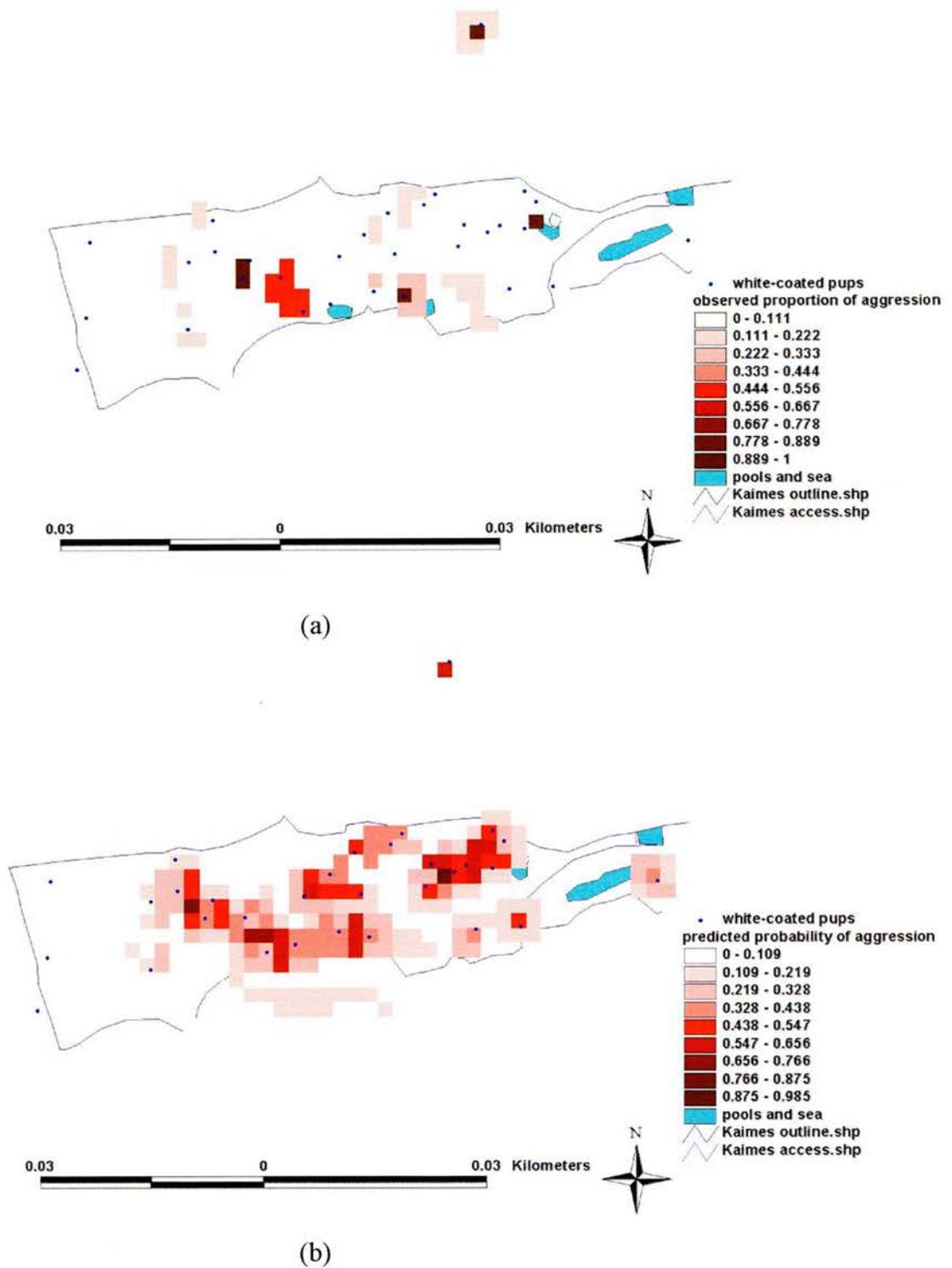


Figure 5.3.8: The observed proportions of aggression (a) and the predicted probabilities of aggression (b) occurring on the 20 November 2000 for each cell given its habitat type.

Model fitted to the presence/absence of newborn pups (see Appendix 3):

A model was firstly fitted to the presence/absence of newborn pups using only the topographical parameters and the preceding white-coated pup distribution. The fitted versus observed plot indicated that many of the fitted values were much lower than the observed values. This was again demonstrated when probabilities of newborn pups were fitted to each cell on the grid for three dates during the breeding season (Figures 5.3.10-5.3.12). All were from before Day 19 of the study period because few pups were born after this. Although the highest probabilities coincided with where pups were born, particularly on the first and second date, the number of cells with high probabilities was very low (Figures 5.3.10-5.3.12).

When the probability of aggression was included as a variable, the cells for all days were binned into 1925 habitat categories. Newborn pups were observed close to access to the sea, but less often within the first 10m from the access point (Figure 5.3.9). They were generally close to water sources, on slopes up to 25°, in habitats with other pups present and with pups in neighbouring cells (Figure 5.3.9). There appeared to be more pups born in habitats with a low probability of aggression. Few pups were born after Day 20 of the observation period. The fitted GLM retained all of the above variables along with a number of polynomial and second order interaction terms. Including aggression in the model improved the fitted versus observed plot.

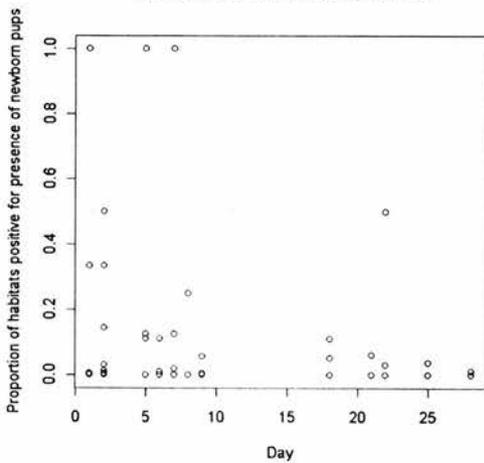
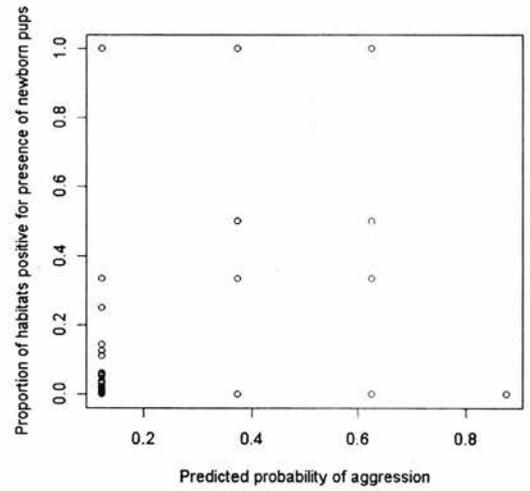
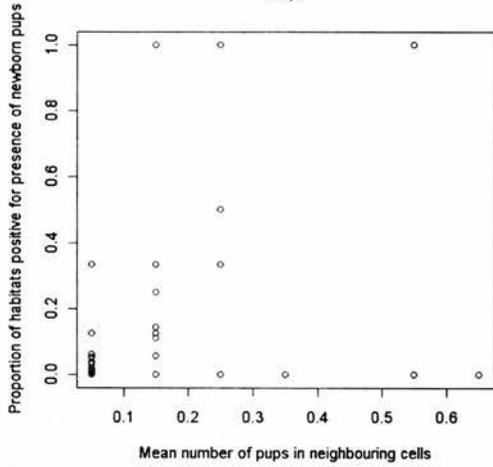
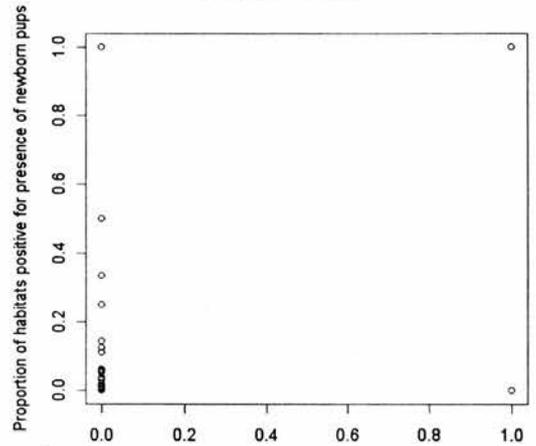
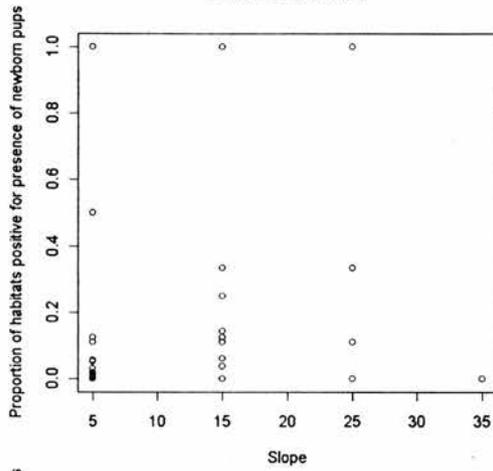
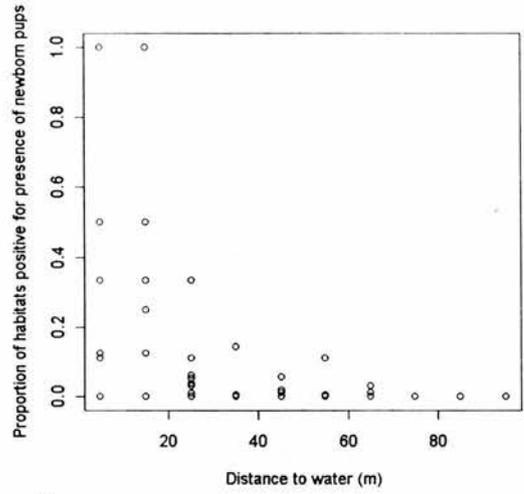
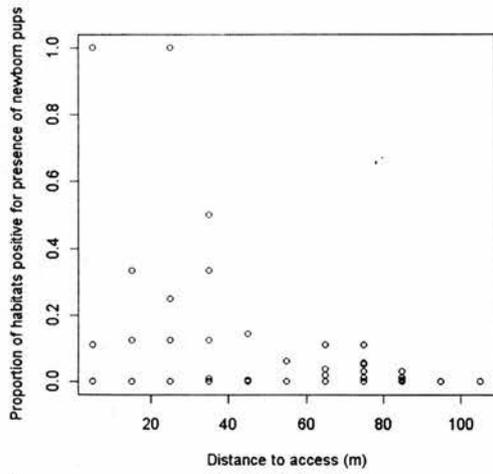
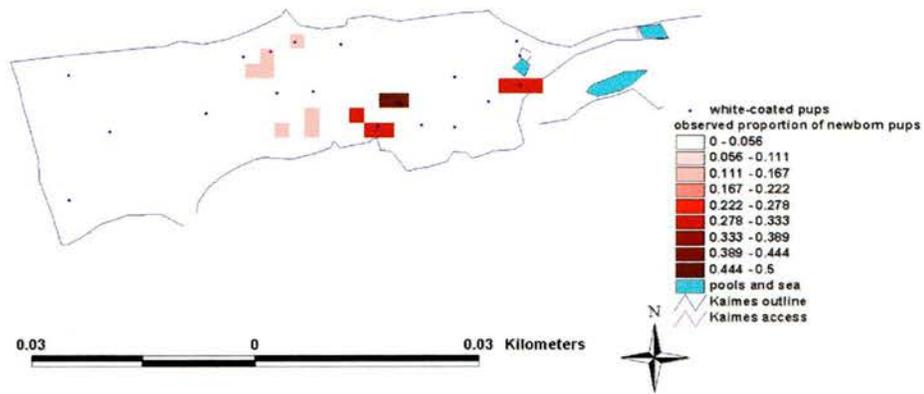
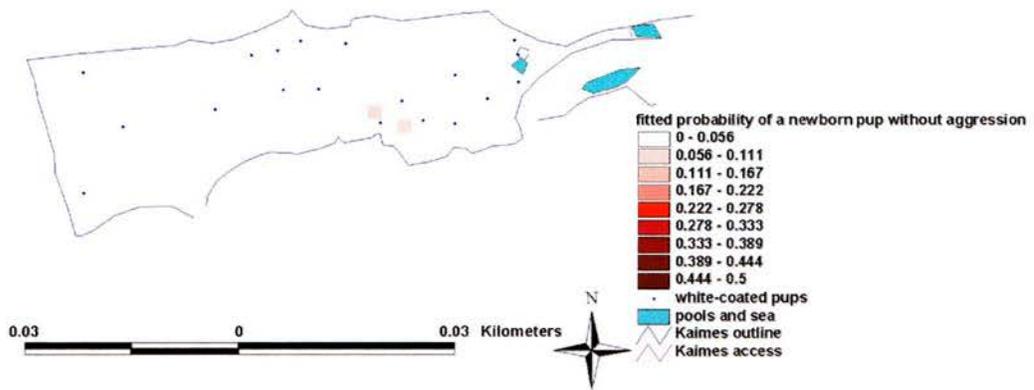


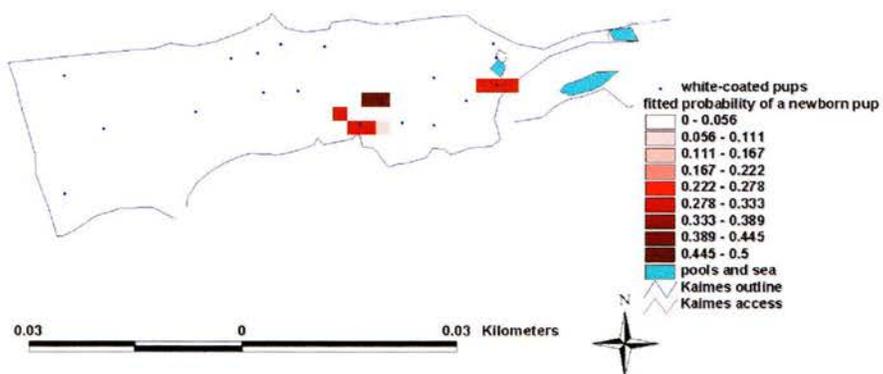
Figure 5.3.9: The proportion of each habitat type that is positive for newborn pups against each explanatory variable for every day of observations on Kaimes, Isle of May, 2000.



(a)

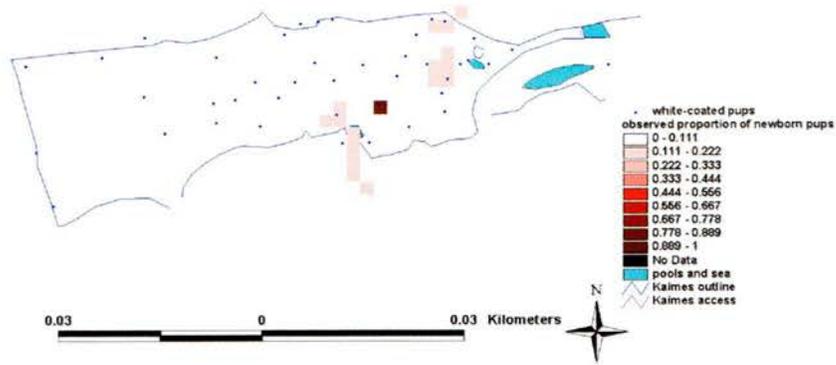


(b)

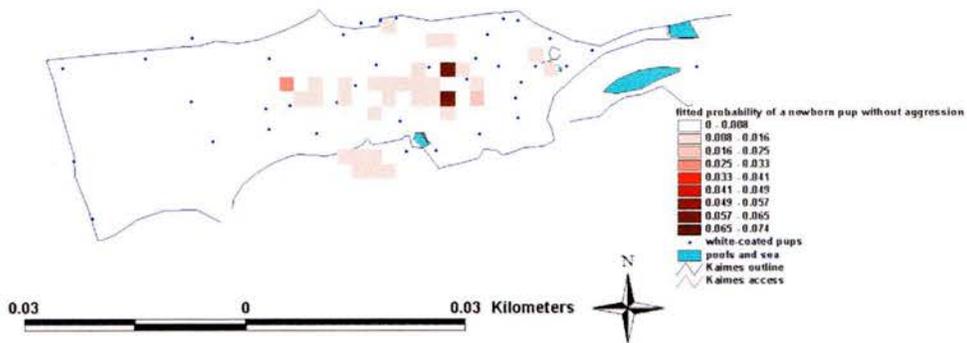


(c)

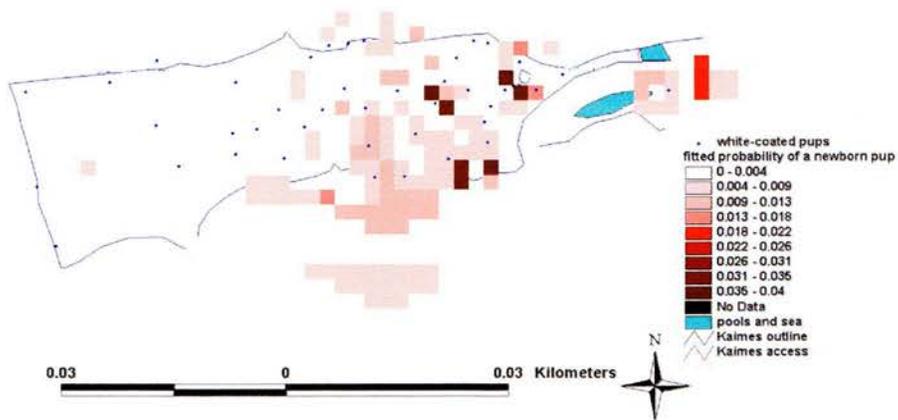
Figure 5.3.10: The observed proportions of pups born in each cell given its' habitat type (a) and the fitted probabilities of pups being born in each cell firstly using a model without aggression (b) and then using a model with aggression included (c) on the 1 November 2000 given the habitat types from the 31 October 2000.



(a)



(b)



(c)

Figure 5.3.11: The observed proportions of pups born in each cell given its' habitat type (a) and the fitted probabilities of pups being born in each cell firstly using a model without aggression (b) and then using a model with aggression included (c) on the 6 November 2000 given the habitat types from the 5 November 2000.

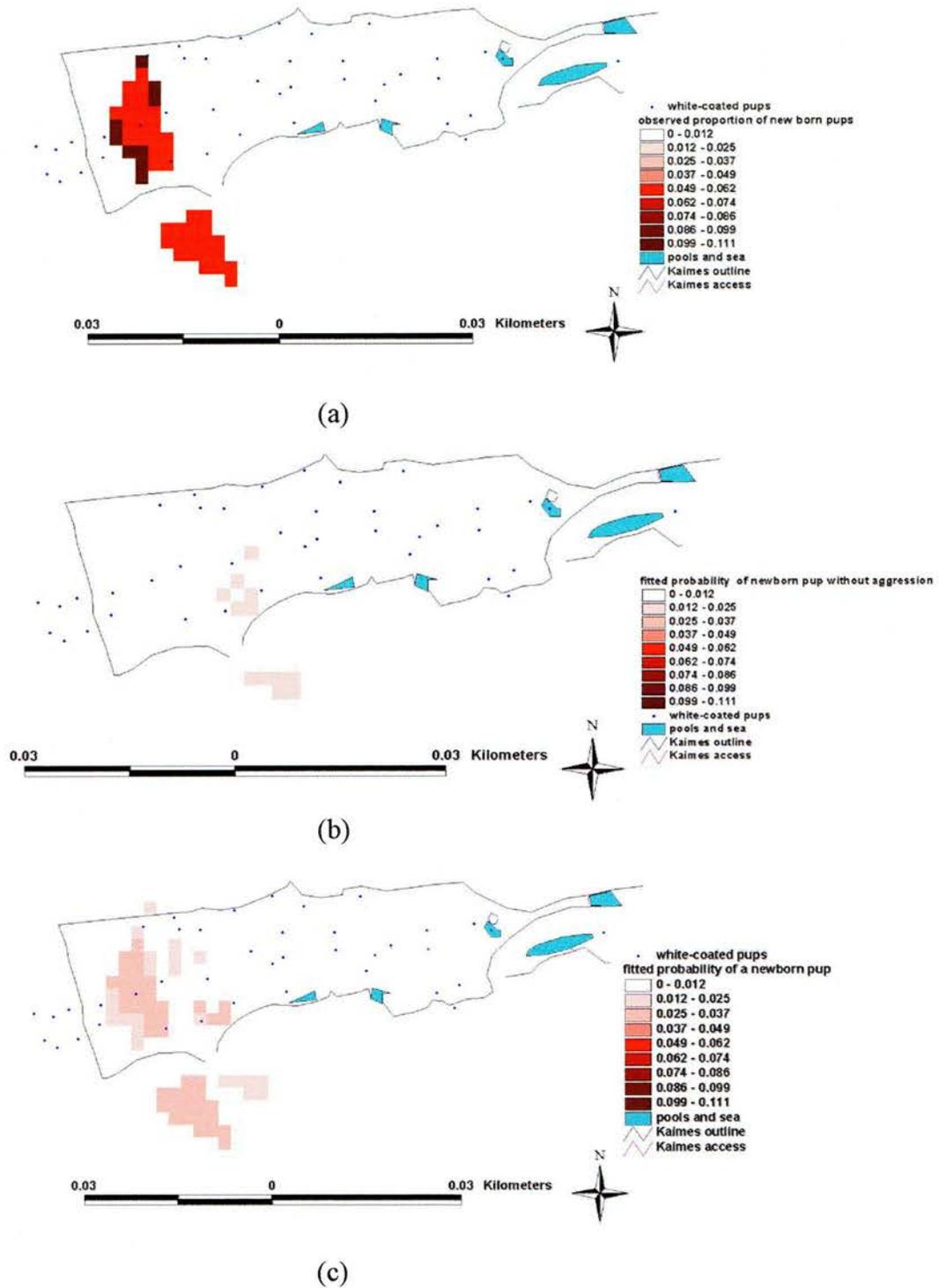


Figure 5.3.12: The observed proportions of pups born in each cell given its' habitat type (a) and the fitted probabilities of pups being born in each cell firstly using a model without aggression (b) and then using a model with aggression included (c) on the 17 November 2000 given the habitat types from the 16 November 2000.

Although pup presence was the only significant single variable, all the other variables had significant interactions of some kind (Table 5.3.2). In the fitted GLM, the probability of a pup being born in a particular habitat decreased with increasing distance to water, slope, an increasing number of neighbouring pups, an increasing probability of aggression and day. It increased with increasing distance to access and the presence of pups in a habitat. Three examples of the distribution of the fitted probabilities of newborn pups are shown alongside the observed distribution of newborn pups and the fitted probabilities from the model with no aggression included (Figures 5.3.10-5.3.12). In all three examples the locations of the fitted probabilities strongly coincided with the observed distribution of newborn pups. Inclusion of aggression as an explanatory variable improved model fit although the values of the fitted probabilities were generally lower than the observed proportions.

Table 5.3.2: The significance of the variables included in the GLM fitted to the daily locations of newborn pups. The significance of all individual variables is shown but only significant interaction terms have been included.

Explanatory variable	Significance . 0.1 * 0.05 ** 0.01 *** 0.001	Explanatory variable	Significance . 0.1 * 0.05 ** 0.01 *** 0.001
Distance to water (m)		Slope:Day	***
Distance to access (m)		Slope:Day ²	***
Slope		Men number of neighbours:Pup presence	.
Mean number of neighbours		Mean number of neighbours:Day ²	***
Pup presence	*	Mean number of neighbours:Day ³	*
Probability of aggression		Probability of aggression:Day ²	.
Day		Probability of aggression:Day ³	.
Distance to access ²	**	Probability of aggression:Day ⁴	.
Day ³	.	Distance to water:Distance to access:Day	***
Day ⁴	.	Distance to water:Distance to access:Day ³	***
Distance to water:Slope	**	Distance to water:Distance to access:Day ⁴	***
Distance to water:Day	**	Distance to water:Slope:Mean number of neighbouring pups	***
Distance to water:Day ³	***	Distance to water:Slope:Day	*
Distance to water:Day ⁴	***	Distance to water:Mean number of neighbouring pups:Day ³	*
Distance to access:Mean number of neighbours	.	Distance to access:Slope:Day ²	**
Distance to access:Day	***	Distance to access:Slope:Day ²	**
Distance to access:Day ²	***	Distance to access:Probability of aggression:Day ²	*
Distance to access:Day ³	*	Slope:Probability of aggression:Day ³	*
Slope:Pup presence	.	Mean number of neighbouring pups:Probability of aggression:Day ²	*

5.4 Discussion

Modelling the way in which a female grey seal chooses where to give birth on a breeding colony is a good example of a situation where the effects of both spatial and temporal variability should be taken into consideration. On the Isle of May study site, the changing environment faced by females arriving at different intervals was apparent. 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 water source declined over time. This process should occur for most breeding patches 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 habitats 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 presence of white-coated pups, 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; Twiss *et al.*, 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 vacant sites close to access that were made available by the departure of females that had pupped early in the season.

The locations and frequency of aggressive encounters changed over time because of the changing locations and numbers of females. Most of the interactions occurred either in the presence of white-coated pups or where there was a pup in a neighbouring cell, which 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. Aggressive encounters between females were also recorded in locations where pups were not present. These mainly involved females travelling to and from water, or females fighting for space close to water. Although the movements of adult females were recorded during the study period, they were not included in the analysis because they could not be measured from aerial survey photographs.

Aggressive encounters were most frequent between 20m and 60m from the access to the sea. Few encounters occurred within the first 10m from access. The access to the sea for the Kaimes breeding patch is a narrow, steep-sided gully that all females had to pass through at some point to arrive at and leave the colony. The characteristics of the access point meant that it was often congested with females moving to and from the sea, which may have been the reason that very few pups were born close to the access gully. The risk of separation or injury to pups born in this area would have been high.

Most of the aggressive encounters occurred close to freshwater pools within the study area. Many females visited these 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; Twiss *et al.*, 2001). Access to water (either the sea or inland pools) 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 breeding patches such as Kaimes, where there are few pupping sites close to the sea, access to freshwater pools may be sufficient to allow females to stay cool. The costs, 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), for a female visiting these pools were probably lower than travelling to the sea. However, there were additional costs associated with the relatively high levels of aggression recorded around the pools.

The model fit to the presence or absence of aggression was reasonably good. The model performed equally well throughout the study period and over a range of different habitat types. When the model was used to fit or predict aggression for a particular day there were a number of cases of over-prediction in cells that contained a pup or had a pup present in a neighbouring cell. However, observations were only made for six hours each day, and aggressive interactions may have occurred in these cells during the unobserved 18 hours.

It is not surprising that the precise location at which pups were born was not predicted particularly well by a model that used only topographical variables. However, the number of social and behavioural variables that could be included in the model was limited to those variables that can be measured from aerial survey photographs. This analysis has shown that the presence of aggressive interactions can be accurately predicted from information on topography and the distribution of white-coated pups, all of which can be extracted from the aerial surveys.

There are many other behavioural or social characteristics of a grey seal breeding patch 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 patch (Pomeroy *et al.*, 2000b). The Isle of May has only been colonised since the 1970's, and Kaimes has only been used since the late 1990's. Newly colonised breeding patches are often occupied by young, often primiparous, females who are unable to compete for space in their natal breeding patch. One of the advantages of using Kaimes as a study site was that the effects of matrilineal social organisation were likely to be limited in such a new patch. Therefore, the pupping site choices observed in this study were more likely to be based on topography and the presence of conspecifics rather than on complex social factors.

The fit of the model to the locations of newborn pups was generally good throughout the season. The habitats with the highest probabilities of a pup being born matched

those that had the highest proportions of newborn pups. The main difference between the observed and the fitted distributions was that the fitted probabilities were generally lower than the observed proportions.

Although the coefficient for the predicted probability of aggression in the model of newborn pup position was not significantly different from zero, a number of the interaction terms that included aggression did have significant coefficients. In particular, the coefficient for the interaction between aggression and time was significant. The probability that a pup would be born in a habitat where there was a high probability of aggression decreased as the season progressed. This may have been because more space became available later in the season, allowing pregnant females to choose pupping sites away from other females, where there was less chance of aggression. The significant interaction between time, aggression and presence of neighbouring pups provides further evidence for this. Females giving birth later in the season are thought to be younger, less experienced animals that cannot compete successfully with older females for the best pupping sites (Twiss *et al.*, 2000b). It is likely that the only way younger females can occupy pupping sites relatively close to the access point or an inland pool is by pupping late in the season.

White-coated pups are thought not to move far from their birthplace, but pups were often seen wandering short distances when their mother had gone to a pool or the sea. As a result, pups often moved from one 2m x 2m cell to a neighbouring cell between days, but usually this did not result in a change in habitat category.

However, on a few occasions a pup was born in a cell that had been occupied by a different pup on the previous day. This could result in a positive relationship between the presence of a pup in a cell on one day and the probability of a pup being born in that cell on the following day. Although it is unlikely that a female would give birth in a cell where a pup was already present, this relationship is not totally unrealistic.

The fitted GLM indicates that there are two mechanisms that may regulate the density of seal pups within a patch: aggression between females, and the fact that the probability of a pup being born in a cell decreased as the number of pups in neighbouring cells increased.

The effects of topography on the positions of newborn pups were as expected, with the exception of distance from access to the sea. The model predicted that the probability of a pup being born in a cell would increase as distance to the access point increased. This relationship is probably an artefact of the particular topography of the study site. Few pups were born within 10m of the only access point at Kaimes. This was probably due to the large amount of traffic in this area. As a result, the model fitted a positive relationship between distance to access to the sea and the probability of a pup being born. This relationship is unlikely to be observed at a patch with a wide access point to the sea, and the coefficient for this variable may have to be adjusted when applying the model to patches with different types of access point.

In both models, time was a significant explanatory variable and was also involved in a number of significant interaction terms. However, the effect of time was rarely linear, as indicated by the lack of significance of day in both models. It was the second, third and fourth order polynomial terms for day that were retained in both models and that were involved in significant interactions.

The spatio-temporal model developed here for predicting where female grey seals will give birth to their pups during a breeding season, provides a means for identifying and quantifying suitable pupping sites within other patches using only data extracted from aerial photographs. This study has demonstrated the value of including information on temporal, behavioural and social variation as well as topography in modelling a dynamic system.

Chapter 6

Assessing the Predictive Power of Spatio-Temporal Models of Pup Distribution.

6.1 Introduction

Developing ecological models for predicting the likely distribution of a species is of little use if the predictive power of these models is not or cannot be tested (Fielding and Bell, 1997; Pearce and Ferrier, 2000; Verbyla and Litaitis, 1989). Evaluating model performance assists in determining how suitable a model is for a range of applications (Pearce and Ferrier, 2000). There are two approaches that are used for evaluating the predictive power of a model: using a calibration data set and then jack-knifing or bootstrapping with these data; or using two independent data sets, one for calibration and the other for evaluation (Guisan and Zimmermann, 2000).

In this study I used data collected during an observational study of a grey seal breeding patch on the Isle of May (Scotland) as the calibration data set to which models were fitted (Chapter 5). The predictive ability of these models was initially assessed visually, using observational data from days in the breeding season that were not included in the model fitting process. In this chapter, the same models are used to predict the distribution of pups on breeding patches other than the Isle of May to test their generality. The development of a technique for rectifying and tessellating the SMRU aerial survey data set (Chapter 3) provided a range of potential evaluation data sets. Because aggressive behaviour cannot be measured in the aerial photographs, only the model predicting the presence of newborn pups could be evaluated in this way.

There are two general classifications of prediction error that may be observed when comparing the observed with the simulated distribution: algorithmic errors and biotic errors (Fielding and Bell, 1997). Algorithmic errors are associated with the model fitting and data-gathering process. Biotic errors occur when not all of the ecologically-relevant processes have been included in the model (Fielding and Bell, 1997). As the number of processes that could be included in this study was restricted to those that are measurable in aerial photographs, biotic prediction errors are a possibility. In presence/absence models there is the possibility of false positive or false negative predictions but in a probabilistic model with binary data, such as is the case in this study, the probability of a false positive or negative is determined by the threshold probability at which a prediction is accepted as being a presence.

There are a number of problems associated with assigning a threshold probability for accepting a prediction as presence. Guisan and Zimmerman (2000) describe methods for improving the threshold so that it relates to the scale of the observations, but the resulting presences/absences are still dependent on the choice of threshold and therefore may include some bias. There is the potential for large numbers of cells to have similar habitat characteristics and as the models are based on habitat categories, large numbers of cells may generate similar prediction values. If this is the case and the habitat is unsaturated, many cells may be classified as false positives (suitable but unoccupied) because they have the potential to become positive should the population expand. However, this will degrade the perceived performance of the model. Therefore, it was

decided to adopt a different approach using simulation and maximum likelihood methods.

Testing the likelihood of the observed pup distribution occurring under the simulation model compared to the likelihood under a null model, where the probability of a pup being born in a cell is equal across a breeding patch, is a more general test of predictive ability. The observed pup distribution extracted from a particular set of aerial photographs depends on the sequence of females giving birth and of pups leaving the patch prior to the date of the aerial survey. A dynamic approach, simulating the sequence of female arrival and pup departure, was used to generate pup distributions that were directly comparable to the observed distributions. Only the distribution of pups in stages 1-3 (see Chapters 2, 3 and 4) were extracted from the photographs, therefore “departure” of a pup occurred when it moulted its white coat and passed into stage 4. Time to complete the moult has been documented by Duck *et al.* (submitted), but time to the start of the moult has not. However, an observational study carried out on the island of North Rona by Paula Redman (pers comm.) provided 36 observations of time from birth to the start of the moult. This ranged from 11 to 19 days with a mean of 15 days. This dataset, along with the counts of stage 1-3 pups from the aerial photographs, provided the basis for a pup production curve that was used in the simulation of the arrival and departure of pups from a patch. The likelihood of obtaining the observed distribution of pups was calculated for three dates during the 1999 breeding season for each study site.

6.2 Methods

Study sites:

Two of the breeding patches in Orkney (Cornholm and Ruskholm) that were used to examine topographical preferences in Chapter 4 were used to test the predictive power of the two models developed in Chapter 5. To assess the models' performance at different stages of the breeding season, three aerial survey dates for each island were chosen to represent early, middle and late periods during the 1999 breeding season.

Extraction of data from aerial photographs:

The aerial survey photographs were digitised, orthorectified and tessellated in the manner described in Chapter 3 to allow the extraction of topographical and pup distribution data. Only the locations of pups in stages 1-3 (white-coated pups) were extracted from the images. The habitat variables in the models (distance to water, distance to access, slope, pup presence and mean number of neighbouring pups) were all either extracted directly from the images or generated using a GIS as described in Chapter 3 and Twiss *et al.* (2000). Each variable surface was generated at a 2m x 2m cell resolution.

Generating pup production curves:

For each patch, the number of stage 1-3 pups counted on the three aerial survey dates was used to estimate a pup production curve (see Duck *et al.*, submitted), which was used to calculate the number of pups born on each day of the breeding season. A spline was fitted to the three counts plotted against day of the breeding

season, assuming that no pups were born prior to 27 September 1999 and no pups were born after 1 January 2000. The predicted number of pups present each day was rounded down to the nearest whole number. The number of pups born on a given day is the difference between the number present on that day and the number present on the previous day plus the number of pups that began moulting on that day.

Generating pup distributions:

The aggression model developed in Chapter 5 was used to predict the level of aggression that a female seal would experience in each cell on the day before the first birth using the habitat characteristics of that cell. This level of aggression was then incorporated into the model to predict the probability that a pup would be born in that cell on the following day. The predicted number of pups born on that day were 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 value randomly sampled from the 36 observations. The mean number of neighbouring pups was calculated based on the new pup distribution. The aggression model was then reapplied using the updated variables to predict the level of aggression anticipated on the following day, and the probability of a pup being born in each cell on that day was calculated. This process was repeated until the third survey date of the breeding season was reached. Pups were removed from the distribution once they had reached the assigned time to moult value. The positions of pools of water within a patch (and therefore the distance to water surface) changed over the course of the breeding season because of rainfall. It was not possible to track the changes

in the distribution of these pools that occurred between surveys. Instead, the distribution of pools on a particular day was assumed to be the same as that recorded in the previous aerial survey until half the total rainfall recorded between surveys by the nearest meteorological recording station in Orkney (Met Office, pers comm.) had fallen, at which point it was updated to the distribution observed on the next survey.

Testing the likelihood of the observed data occurring under the simulation and null models:

When the simulation process reached each of the three survey dates, the predicted pup distribution was saved. This entire process was replicated 30 and 60 times to generate a frequency of occupancy for each cell, which was divided by the number of replicates to give a predicted probability of occupancy. There was no significant difference found between 30 and 60 replicates on any of the three survey dates (paired t-test, survey 1: $t = 0.42$, $p = 0.67$, survey2: $t = 0.78$, $p = 0.44$, survey3: $t = 0.79$, $p = 0.42$), therefore 30 replications were considered sufficient in the remainder of the simulations. Thirty realisations of a null model, in which the probability of a pup being born was identical for all the cells within a patch, were also generated for each survey date. The probability distributions derived from the simulation model and the null model always included a large number of cells with zero probability of occupancy. To allow likelihood values to be calculated for both surfaces, the zero probabilities had to be replaced with a probability that was lower than any probability generated by either model. After the zero probabilities had been replaced, the values for each cell were rescaled so that they summed to one. Values for the likelihood of the observed pup

distribution occurring under the null model and the simulation model were calculated by summing $\log(p)$ for those cells observed to be occupied, where p is the probability value for each cell. This was repeated using 200 different probabilities between 2×10^{-2} and 2.74×10^{-27} to replace the zero probabilities. Values of Akaike's Information Criterion (AIC) were calculated for each log likelihood and for each survey date and compared. The model with the lower AIC value was considered to provide the best fit to the observed data.

Application of a model excluding “distance to access”:

The relationship between distance to access and pup location was shown in Chapter 4 to vary between breeding patches and survey dates. To test whether omitting the distance to access variable improved the generality of the model, the above methods were repeated for Cornholm in 1999 using models fitted to the Isle of May observational data with the distance to access variable excluded.

6.3 Results

Comparison of simulated and observed distributions:

Cornholm 1999

On the first survey of the 1999 breeding season most pups were observed around the coast, whereas the simulation model predicted that the cells with the highest probability of occupancy were those around a pool of water in the northwest corner of the island (Figure 6.3.1a and b). However, by the second and third surveys, the simulated distribution of probabilities resembled the observed pup distribution much more closely (Figure 6.3.1c-f). Areas of high predicted probability were found around the coast and at a number of inland areas.

Ruskhalm 1999

On the first survey, the highest predicted probabilities of occupancy were concentrated in inland areas and no pups were predicted to be born around the coast where most pups were in fact observed (Figure 6.3.2a and b). However, pups that were born inland were found in cells with a high probability of occupancy under the simulation model. By the second and third surveys, coastal areas and inland areas had a high probability of occupancy and there was a much closer match between the predicted and observed distributions (Figure 6.3.2c-f).

Cornholm 1999 excluding “distance to access”

When “distance to access” was excluded from the model the simulation produced different probability distributions for each survey date (cf Figures 6.3.3a, c and e with Figure 6.3.1a, c and e). For the first survey, the simulated probabilities

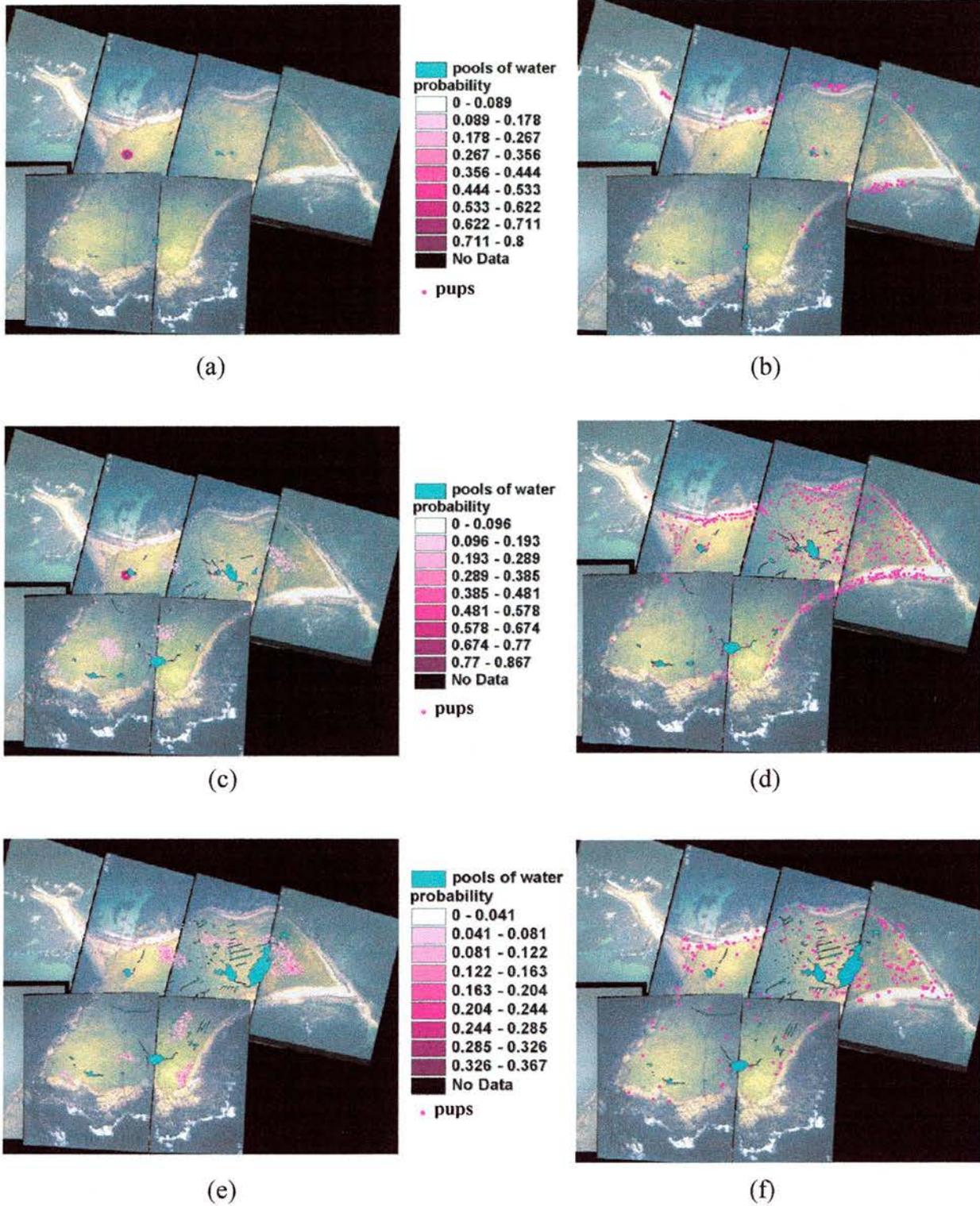


Figure 6.3.1: The simulated probabilities of occupancy (a, c, e) and the observed pup distributions (b, d, f) for survey 1 (a and b), survey 2 (c and d) and survey 3 (e and f) on Cornholm in 1999.

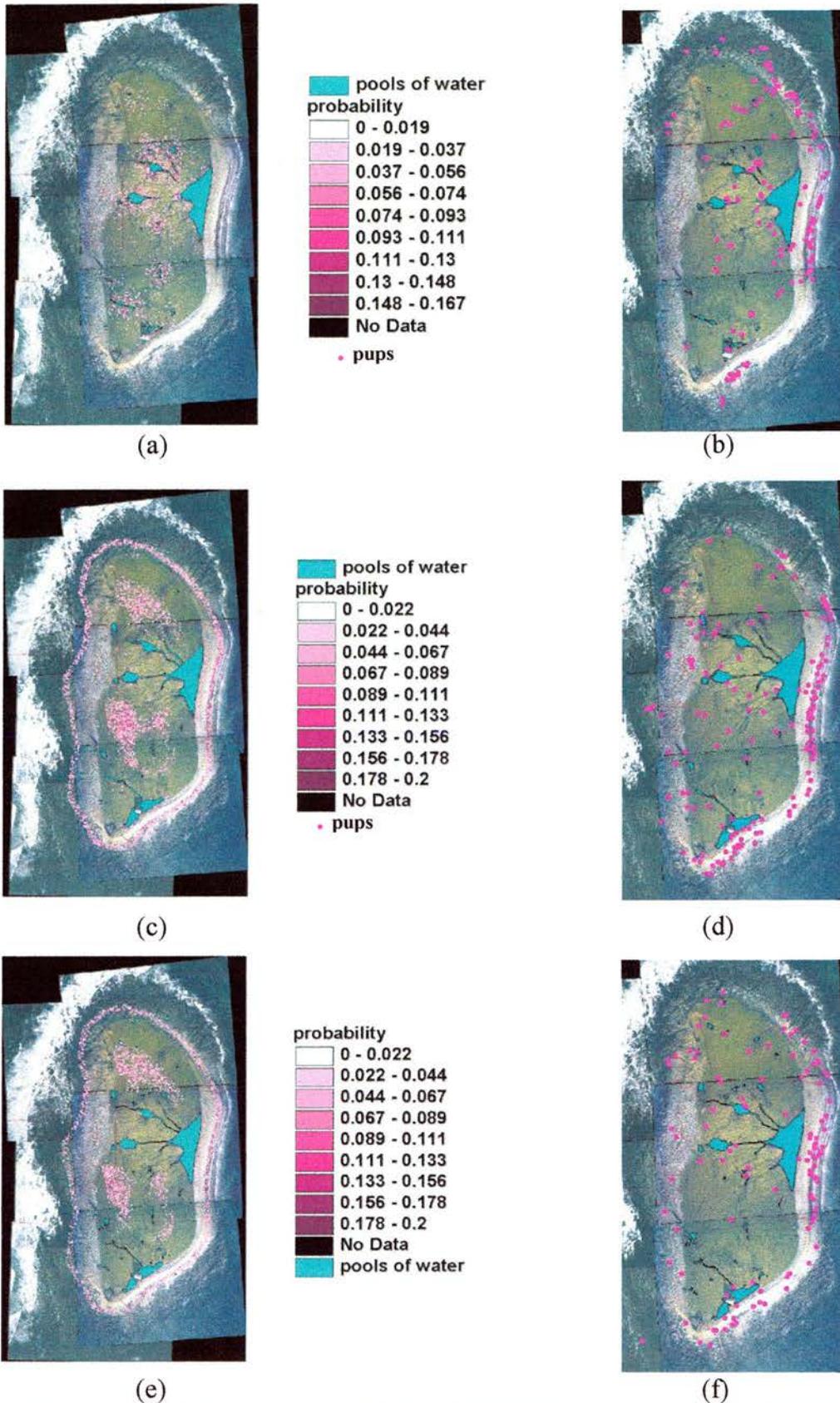


Figure 6.3.2: The simulated probabilities of occupancy (a, c, e) and the observed pup distributions (b, d, f) for survey 1 (a and b), survey 2 (c and d) and survey 3 (e and f) on Ruskholm in 1999.

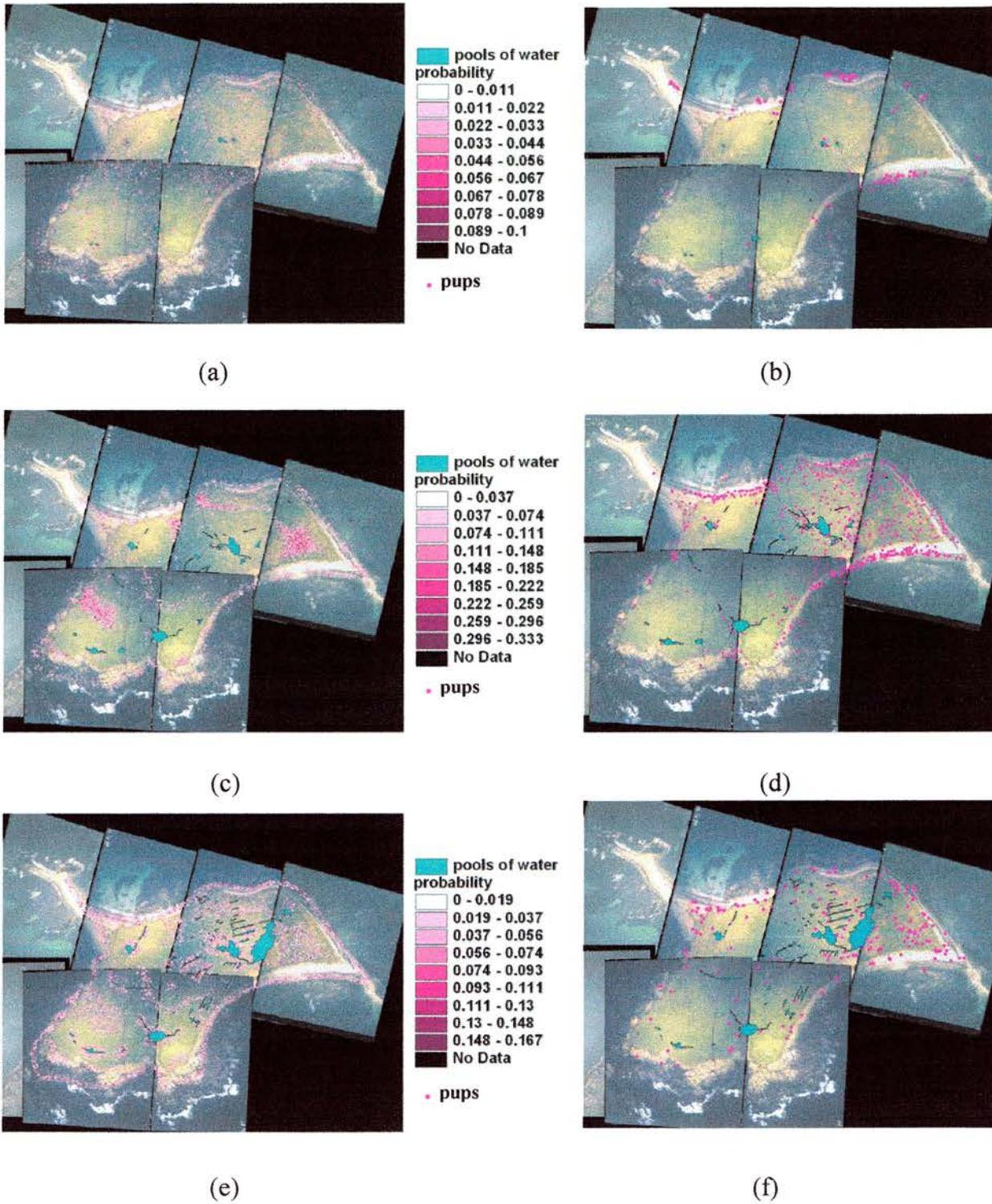


Figure 6.3.3: The simulated probabilities of occupancy (a, c, e) and the observed pup distributions (b, d, f) for survey 1 (a and b), survey 2 (c and d) and survey 3 (e and f) on Cornholm in 1999 with distance to access excluded from the models.

were spread throughout the island and no areas were highlighted as being particularly suitable (Figure 6.3.3a). By the second survey, cells with a high probability of occupancy were concentrated around the coast and in a small number of inland areas (Figure 6.3.3c). The predicted probabilities most closely resembled the observed pup distribution on the third survey, where the distribution of probabilities was both coastal and around the inland pools of water. For this survey, there was a mismatch at the western end of the island where a number of cells were predicted as having a high probability of occupancy but very few pups were observed (Figure 6.3.3e and f).

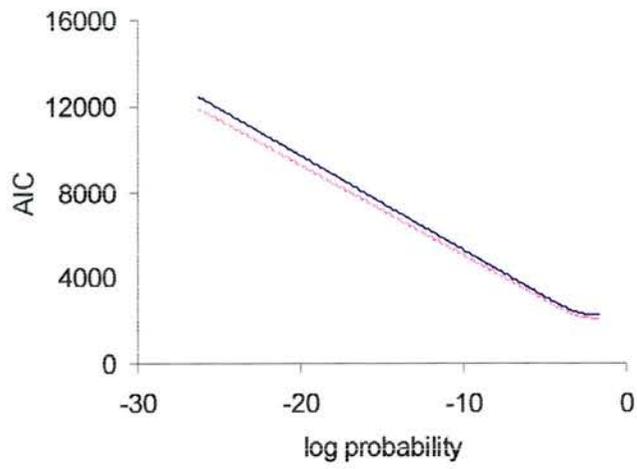
Comparison of simulated and null models:

Cornholm 1999

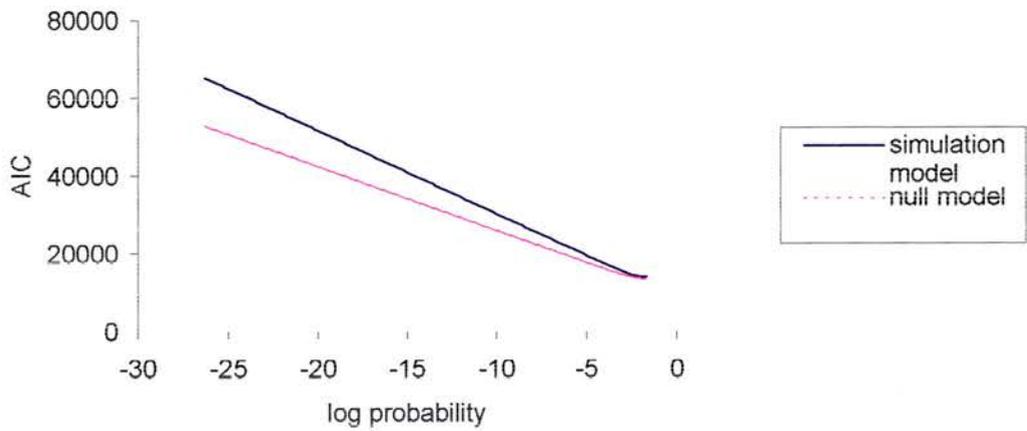
For each of the three survey dates on Cornholm in 1999, the AIC value for the null model was lower than for the simulated model across all replacement probability values (Figure 6.3.4). The difference in the ability of the two models to predict the observed pup distribution was most pronounced for the second survey. The difference between the AIC values for the two models decreased as the replacement probability increased in all cases.

Ruskhalm 1999

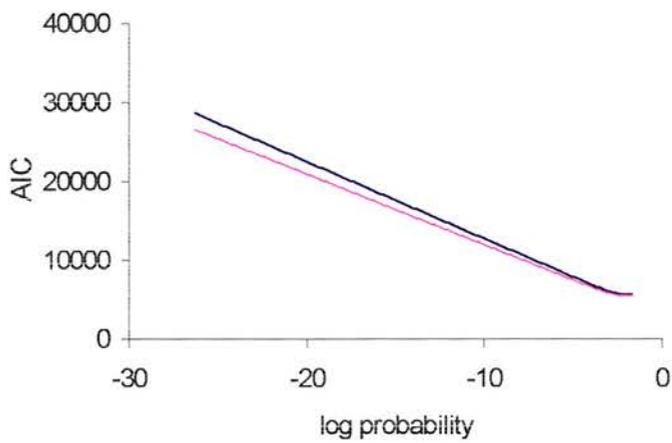
For the first survey of Ruskhalm, the AIC value for the null model was lower than for the simulated model across all replacement probability values (Figure 6.3.5a). For the second and third surveys, the AIC values for the simulation model were lower than for the null model at probability values less than 1.5×10^{-3} and 6.34×10^{-3} respectively (Figure 6.3.5b and c).



(a)



(b)



(c)

Figure 6.3.4: AIC values comparing the likelihood of the observed Cornholm 1999 distribution occurring under the simulation model and the null model over a range of probabilities that replaced zero probabilities for (a) survey 1, (b) survey 2 and (c) survey 3.

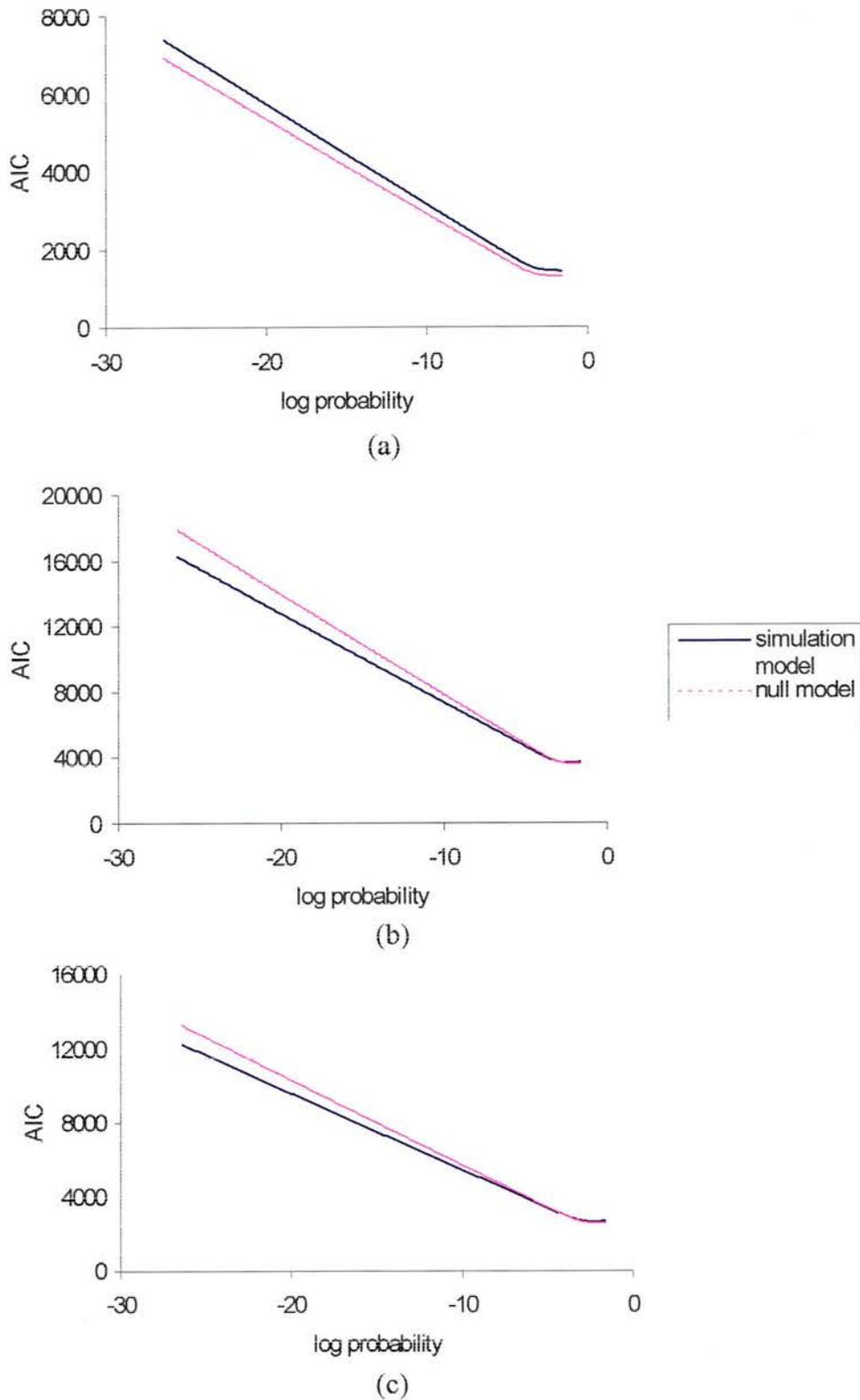
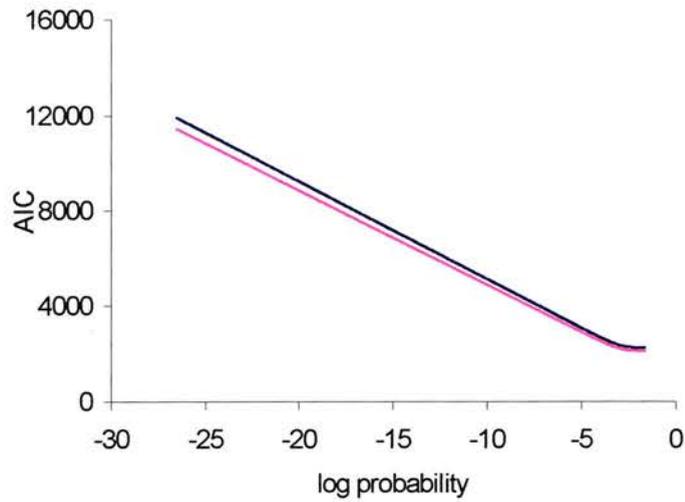


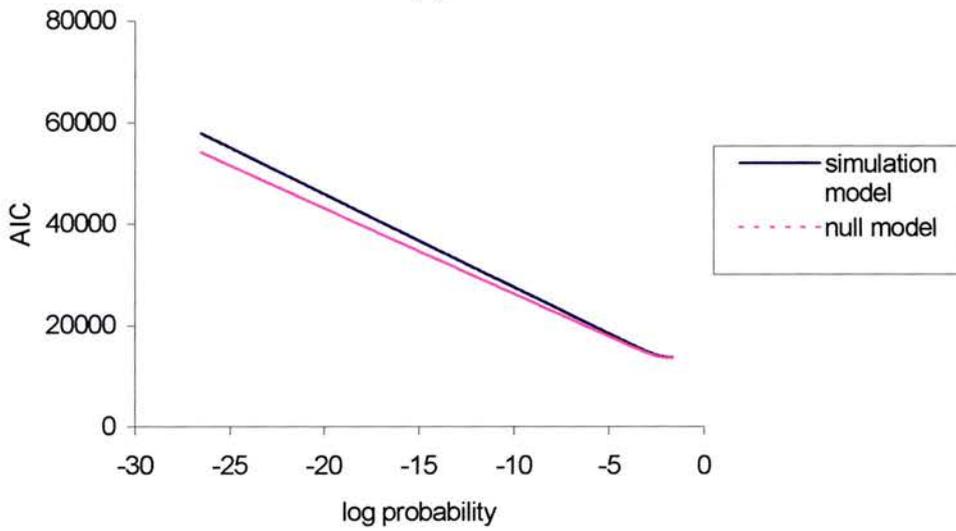
Figure 6.3.5: AIC values comparing the likelihood of the observed Ruskholm 1999 distribution occurring under the simulation model and the null model over a range of probabilities that replaced zero probabilities for (a) survey 1, (b) survey 2 and (c) survey 3.

Cornholm 1999, excluding “distance to access”

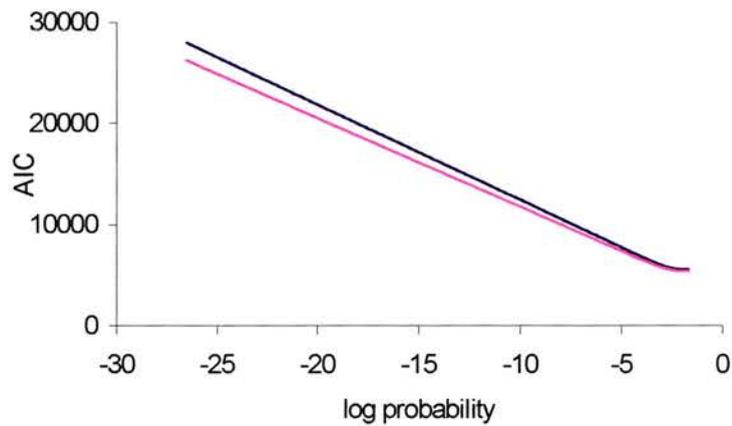
When distance to access was excluded from the simulations, the AIC value for the null model was lower than for the simulated model across all replacement probability values (Figure 6.3.6), although the difference was less than that observed with the full model (Figure 6.3.4). The difference between the AIC values for the two models decreased as the replacement probability was increased.



(a)



(b)



(c)

Figure 6.3.6: AIC values comparing the likelihood of the observed Cornholm 1999 distribution occurring under the simulation model with distance to access excluded and the null model over a range of probabilities that replaced zero probabilities for (a) survey1, (b) survey 2 and (c) survey 3.

6.4 Discussion

The predictive applicability of the models developed in Chapter 5 appeared to be limited when they were applied to islands such as Cornholm and Ruskholm in Orkney. The greatest mismatch between the predictions made using simulation and the observed distributions was for the first survey date, when areas with low distance to access values (ie. close to the coast) were predicted to have a low probability of occupancy. The probability that these areas were occupied increased over time so that coastal areas were predicted to have a relatively high probability of occupancy by the second and third surveys.

On Cornholm, in particular, the low predicted probability of occupancy for cells close to the access points resulted in the null model out-performing the simulation model. This failure may be an artefact of the topographical features of the study site on the Isle of May where the data used to parameterise the models were collected. On that study site, the only access point to the sea was a narrow gully. This restricted the number of pups that could be born close to access. In addition, the period of time over which data for this site were collected was limited by the arrival and departure dates of the fieldwork team from the Isle of May. As a result, the locations where the first pups were born could not be determined. For these reasons, the coefficient of the predicted relationship between distance to access and the probability of a pup being born in a cell was positive. Although this relationship provided accurate predictions of the locations of newborn pups at the Isle of May study site on days that were not

included in the model-fitting process (Chapter 5), it was of limited applicability for breeding patches where there are large areas of access to the sea.

Excluding distance to access from the predictive model did not improve its performance relative to the null model. Even though the null model predicted a low probability of occupancy in every cell, the fact that most pups born early in the season were found around the coast, where the simulation model predicted a very low, or zero, probability of occupancy resulted in an improved performance for the null model.

Visual assessment of the distributions (Figure 6.3.1 and Figure 6.3.3), indicate that the models with distance to access excluded performed better than the models that included distance to access, particularly for the second and third survey. The models with distance to access excluded predicted relatively high probabilities of occupancy around the coast, which is in agreement with the observations. With a few exceptions, the inland areas that were predicted to have a high probability of occupancy, also agreed with the observed distributions. Although excluding distance to access did not reduce the simulation model AIC value below that of the null model, the locations of the predicted probabilities corresponded more closely to the observed pup distribution.

Both biotic and algorithmic errors probably influenced the performance of the model in predicting pup distribution in Orkney. Biotic errors were always likely to occur because only variables that could be measured from aerial photographs were included in the analysis. Behavioural factors, such as reduced

aggression between related females, are thought to play a role in the choice of pupping sites by females in established breeding patches (Pomeroy *et al.*, 2000b) but are probably less important in relatively new patches, such as those on the Isle of May. Although the exclusion of such behavioural factors from the model may have affected its performance in established areas of a colony, it should have provided realistic predictions at the leading edge of the spread of an expanding breeding patch, which was the main area of interest of this study.

Algorithmic errors are likely to be responsible for the majority of the prediction error. Even though habitat availability was taken into account in the model-fitting process, the limitations associated with the data-gathering process constrained the general applicability of the model. These errors could probably be reduced by reparameterising the model with data collected throughout the breeding season on a study site with topography that is more similar to the expanding breeding patches in Orkney.

In all cases (Figures 6.3.4 – 6.3.6) the difference in the AIC value between the simulation model and the null model decreased as the replacement probability increased. This was due to the rescaling of the probability surface to equal one after the replacement probability was included in the surface. As the replacement probability increased, the height of any peaks in the simulated probability surface was lowered by rescaling, which increased its similarity to the null model surface.

Assessing the performance of a species distribution model using statistical criteria such as the AIC may not reflect the overall applicability of the model. The intended application of the model may be more relevant in defining the models performance than statistics (Fielding and Bell, 1997; Guisan and Zimmermann, 2000). The AIC penalises the performance of a model based on the number of variables included in a model. In this study, the simulation model contained a large number of variables due to the complex interaction terms incorporated, therefore it was heavily penalised compared to the null model which only had one variable (the number of cells in the patch). This may make it difficult for the simulation model to out-perform the null model when they are compared statistically, even when visually the simulation model predictions appeared to be more realistic than those of the null model.

In conclusion, although the predictive ability of the models fitted to the Isle of May data was limited, particularly at the start of the breeding season and when distance to access was included as a variable, the model did provide a reasonable prediction of the use of inland areas towards the middle and end of the season on Cornholm and Ruskholm, when numbers of pups are highest. It may therefore provide an insight into the locations of habitat that may be colonised in the future.

Chapter 7

General Discussion

7.1 General Discussion

7.1.1 Overview of Study:

The development and application of predictive species distribution models based on species-habitat or species-environment relationships has increased in recent years in ecology (eg. Augustin *et al.*, 1996; Beard *et al.*, 1999; Boroski *et al.*, 1996; Buckland and Elston, 1993; Macdonald *et al.*, 2000; Walker, 1990). The increased availability of remotely-sensed data and GIS packages has made accessible suites of environmental data that may be important in determining the observed distribution of a species. One of the most important uses of defining the characteristics of suitable habitat is the ability to predict the distribution of suitable habitat in areas other than the study area to identify locations that may be interesting in terms of both conservation and management. An example of such a study would be the identification of suitable habitat for the reintroduction of beaver (*Castor fiber*) to Scotland based on the habitat characteristics of occupied sites in the Netherlands (Macdonald *et al.*, 2000).

Many of the habitat suitability studies that have been carried out have concentrated solely on factors such as topography, vegetation or climate (eg, Beard *et al.*, 1999; Debinski *et al.*, 1999; Walker, 1990). One study investigating the topographical features of New Zealand fur seal (*Arctocephalus forsteri*) breeding patches around South Island, New Zealand (Bradshaw *et al.*, 1999) identified common topographical characteristics of pup locations across a range of breeding patches. Quantifying the relationship between pup location and topography provided the basis for identifying suitable New Zealand fur seal

breeding habitat in other areas but, as with this study, it was acknowledged that factors other than topography, such as social and behavioural interactions, are likely to play a role in the choice of a pupping site. In the present study, this led to the development of a model, based on the findings of the topographical comparisons, but with aggressive behaviour incorporated as a density-regulating mechanism.

Previous studies that have investigated the factors that may be important in determining where a female grey seal chooses to give birth have predominantly been qualitative rather than quantitative (eg. Anderson *et al.*, 1975; Caudron, 1995; Pomeroy *et al.*, 1994; Redman *et al.*, 2001; Twiss *et al.*, 2000a). The few quantitative studies have not accounted for temporal variations in the availability of suitable breeding habitat that occur within and between breeding seasons. The development of a technique for rectifying and tessellating aerial photographs opened up opportunities for investigating the spatial and temporal variation in the relationships between pup location, topography and the location of conspecifics on a wide range of breeding patches.

Computer simulations of the growth of an idealised grey seal breeding patch that included topographical factors and density regulating mechanisms indicated that the predictions of these models were readily distinguishable from a simple diffusion model and from each other using the kinds of information that could be extracted from aerial photographs of such patches. It was concluded that it would be possible to detect the most important factors determining the choice of pupping sites by female grey seals from aerial photographs.

The development of a method for digitising, rectifying and tessellating aerial photographs, as described in Chapter 3, allowed detailed information on topography and pup distribution to be extracted from current and historical photographs of grey seal breeding patches. Counts of the numbers of pups visible in the orthorectified images were comparable with those made using a microfiche reader, the methodology that is currently used by SMRU to analyse these photographs. Differences in counts between methods, and between counters, were mainly due to differences in the criteria used to classify pups as white-coated or moulted individuals. Topographical information such as distance to access to the sea and distance to pools of water could be extracted from the orthorectified images and used to generate surfaces that could be projected onto Ordnance Survey Digital Elevation Models (DEMs). The time-series of aerial surveys that are conducted each breeding season allowed spatial and temporal variations in the relationship between topography and pup distribution to be investigated. The methodology has limitations, both in terms of its accuracy (which is limited by the accuracy of the available DEMs) and the amount of time required to tessellate the digitised images. However, the quality of data that are made available through this method made it possible to study the mechanisms by which a female grey seal chooses her pupping site on a much greater range of breeding patches than had previously been possible. Until a dedicated photogrammetric aerial survey is carried out of all the major grey seal breeding colonies, the methodology described in Chapter 3 is the most efficient and cost-effective way to extract distributional and topographical information from the existing aerial photographs.

This method has the potential to provide data for a number of different research areas outwith the scope of this thesis. For example, as distance measurements made on an orthorectified image are unbiased estimates of equivalent measurements on the ground, the size of moulted pups in different parts of a patch can be estimated from the aerial photographs (Harvey, 2001). Weaned weight is a reasonable predictor of subsequent pup survival (Hall *et al.*, 2001), and thus could provide a proxy to investigate the relationship between habitat type and breeding success.

Using data extracted from aerial photographs, the relationships between pup distribution and topography were established in Chapter 4 for three breeding colonies in Orkney in the 1999 breeding season and for one colony in the 1993 breeding season. In each year the relationships were examined at the start, middle and end of the breeding season. The resulting relationships were compared to the findings of a similar study carried out on the Isle of May in 1994 (Twiss *et al.*, 2001). With one exception, cells occupied by pups on the Orkney islands were significantly closer to access to the sea and pools of water than unoccupied cells. This is in agreement with the occupancy patterns seen on the Isle of May. On the Isle of May, Ruskholm and Cornholm, there was no significant difference in the slope values of occupied and unoccupied cells. However, on Copinsay, pups were only found within the lower part of the range of available slopes. This may be because the habitat close to access points on Copinsay is predominantly low lying. Until this habitat is saturated, females will probably not move inland to habitats with steeper slopes to give birth.

The distance to water and slope values of occupied cells were similar across islands, years and survey dates once the availability of breeding sites close to access had been taken into account. However, the distance to access values of occupied cells differed between islands, years and survey dates, even when the availability of inland pools of water was accounted for. The inter- and intra-seasonal differences within an island cannot be explained by the characteristics of the access point; they were probably the result of differences in the numbers of pups present. The consistent relationship between pup locations and the distance to water and slope values of occupied cells across patches in different years and at different points within a season indicated that it should be possible to develop a general predictive model of grey seal breeding distribution.

In Chapter 5 a model was fitted to the spatial distribution of aggressive encounters that was observed on a breeding patch on the Isle of May during the 2000 breeding season using topographical parameters and the presence of white-coated pups as explanatory variables. This model was used to predict the probability of aggression occurring over space and time. The predictions from the aggression model were included in a model that was then used to predict the locations of newborn pups. The inclusion of aggression improved the fit of the model when compared to a model that included only topography and the presence of conspecifics. The model fitted the data well both spatially and temporally and therefore was considered to have the potential to identify and quantify suitable pupping sites within other patches using only data extracted from aerial photographs.

The ability of the model to predict pup distributions on different breeding patches was tested in Chapter 6 by simulating the timing and locations of births over a breeding season on two islands in Orkney (Cornholm and Ruskholm) and comparing this with the observed distribution of white-coated pup in aerial photographs. The variables for inclusion in the model were derived from the aerial survey photographs and from an Ordnance Survey DEM. The performance of the simulation model at the start, middle and end of the breeding season was compared with the performance of a null model that assumed all parts of the patch were equally likely to be occupied using AIC to measure the goodness of fit. On both islands, the null model out-performed the simulation model on the first survey date. On the second and third surveys (middle and end of the season), the simulation model performed better than the null model on Ruskholm but continued to perform worse than the null model on Cornholm. The lack of fit between the predictions and the observations, particularly at the start of the breeding season, was thought to be a result of some topographical features of the study site at the Isle of May that was used to calibrate the model. Excluding the distance to access variable from the simulation model improved the fit of the predictions at Cornholm when assessed visually, but did not lower the AIC value sufficiently for it to be deemed better than the null model. In some ways, the visual evaluation of the model fit was more informative than the statistical evaluation, because it was possible to identify where and when the model predictions were most reliable.

7.1.2 Implications of Findings:

This study has quantified relationships between grey seal pup locations and a number of topographical and behavioural factors. Cells within a breeding patch that are currently unoccupied but had a high probability of occupancy in the simulations represent areas that are likely to be colonised in the near future.

Their locations can be used to predict the eventual size and extent of that patch.

As the number of suitable pupping sites in a breeding patch may be the ultimate determinant of local population size, the ability to identify suitable but unoccupied pupping sites in an area may allow estimates of future abundance to be calculated. Estimating potential population size in this way assumes that, as the number of females breeding on a patch increases, density will remain constant. At present, although many local populations may have reached an equilibrium level in pup production, there are still many vacant or partially empty patches for offspring to disperse to. It is thought that although grey seal pups will return to their natal colony to breed for the first time (and all subsequent times), if their anticipated fitness is below some threshold, then individuals will seek out sites at which their fitness is higher (Harwood and Gaggiotti, 1999). Therefore, until a point is reached when fitness is identical in all patches, the density of pups within a breeding patch is likely to remain fairly constant.

We can only speculate on what will happen when all suitable patches are occupied up to the threshold density for fitness-related migration. If this occurs, animals breeding for the first time will have the choice of not breeding at all (and therefore gaining zero fitness) or accepting a fitness level below their current

threshold. Therefore, it becomes very difficult to predict when the UK grey seal population will stop growing, but the findings of this study provide the basis for future studies to make short-term predictions of future local population size in areas such as Orkney.

7.2 Conclusions

In conclusion, I have developed a technique for extracting fine resolution topographical and grey seal pup distribution data from SMRU aerial survey photographs. Relationships established between topographical characteristics and pup distributions over time and space indicated a consistent relationship between pup location and distance to water and slope, but a variable relationship between pup location and distance to access to the sea. Models fitted to observational data collected during the 2000 grey seal breeding season at the Isle of May demonstrated that the occurrence of aggression could be predicted using variables that are measurable in aerial photographs. The locations of newborn pups could be modelled by a combination of topography and variations in the location of conspecifics and aggressive behaviour over time. These models, in conjunction with data extracted from the aerial photographs, were then used to simulate variations in levels of aggression in space and time on two colonies in Orkney. This allowed a density-regulating mechanism to be incorporated into a model to predict pup distribution. The general applicability of the models to breeding colonies other than the Isle of May was limited due to a number of factors associated with the study site, but the model predictions did allow

potential areas of suitable habitat to be identified towards the middle and end of the breeding season, when the number of pups on an island is greatest.

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Appendix 1

Creating a Continuous DEM Surface from Point Data.

The Ordnance Survey Landform Panorama DTM (50m resolution) and the Landform Profile DTM (10m resolution) CD's are used to create Digital Elevation Models for a given OS grid square. This needs to be carried out on a machine that has Microsoft Windows NT, it will not work on Microsoft Windows 2000.

The OS grid squares that SMRU has data for are:

HY40 – Orkney (50m resolution)
HY42– Orkney (50m resolution)
HY44– Orkney (50m resolution)
HY60– Orkney (50m resolution)
HY62– Orkney (50m resolution)
ND28– Orkney (50m resolution)
NY69NE – Isle of May (10m resolution)

These data are in DXF format. The data needs to be imported into ERDAS to be readable. Select “Import” in the main ERDAS menu. Check that “Import” is selected, that “Type” is “DXF to Coverage” and “Media” is “CD-ROM”.

Navigate to input and output directories and click “OK”.

Once importing the data file is complete the original attributes from the DXF file need to be merged back into the point vector coverage (in order to give each point its height attribute). Make sure that there are no points displayed in the Viewer. Open the “Vector Utilities” menu in the main ERDAS menu and select “Build Vector Layer Topology”. Choose the point coverage that was created earlier and make sure that the feature is set to “Point”. Click on “OK” and run the build process which should create a PAT file for the points. Go to “Start Table Tool” in the “Vector Utilities” menu. Open the info file of the point coverage in the Table Tool. This should open a table list of all the tables that are associated with the coverages. Select the *.PAT file of the point coverage. Go

to the “Utilities” menu in the Table Tool and select “Table Merge”. In the “Merge Info Tables” dialogue box do the following:

- Change the “Relate item (key)” to be the *-ID of the point coverage.
- Change the “Join table” to be the *.XCODE Table of the DXF file.
- Change the “Output table name” to be **exactly** the same as the *.PAT file of the point coverage (ie. including the .PAT extension).
- Leave all the remaining fields as the default.

Now run the “Table Merge” process and the height attributes should then be included in the vector attributes. The file should now be ready for the “Surface Tool”. The Surface Tool creates a continuous surface from the point data using interpolation. The Surface Tool is found under “Data Prep – Create Surface”. Click “File – Read” and navigate to the Point Coverage. Select the “Attribute for Z” from the drop-down menu. Click “OK” and then select “Surface” in the main dialogue box and click “Surfacing”. Save the interpolated surface as an *.img file and this can then be used in Orthobase and can also be opened in Arcview 3.2 when the Imagine image support extension is activated.

Appendix 2

Method for Orthorectifying and Tessellating SMRU Aerial Photographs.

Preparation of photographs:

Cut the photographs into singles.

Make an acetate template for putting fiducial marks on the photographs (eg. Figure I).

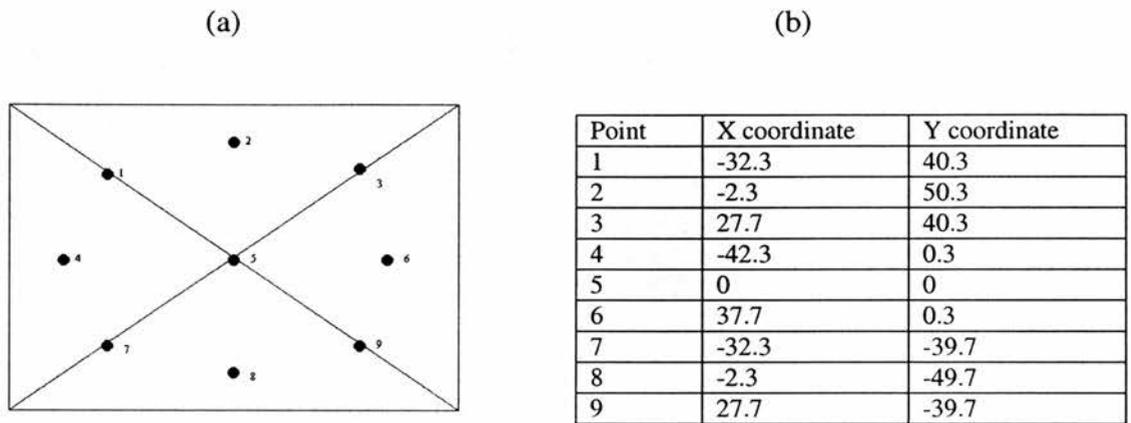


Figure I: The positions on the photograph (a) and coordinates (b) of the fiducial marks.

Mark pinholes on the photographs using the fiducial mark template. The photographs should be placed with the photograph ID number in mirror-image in the top left-hand corner and the template should be placed on top of each photograph in the same orientation with respect to the photograph ID number.

Scan each photograph (with the photograph ID number in mirror-image in the top left-hand corner) using a high-resolution scanner (at 2540 dpi) and save as a Tiff file.

Entering the photographs into ERDAS Imagine:

Make sure the ERDAS dongle is installed.

Start ERDAS Imagine 8.4 and then select the Orthobase icon.

Select "Create a new blockfile" and navigate to the directory where you wish to save the new blockfile.

In the sequence of options that follow choose the following:

- Frame camera
- Set Projection - UK - British National Grid
- Use default projection (Transverse Mercator)
- Use default reference units
- Use default rotation system

Add scanned images to the resulting blank blockfile one by one (Figure II). When all images have been added, click "Edit", select "Compute pyramid layers" and then select "Generate pyramid layers for all images without pyramids". Wait until all pyramid layers are completed.

Entering Interior and Exterior information:

To add interior and exterior orientation information, go to the Frame editor (Figure II) and work through the three tabs (Sensor, Interior Orientation and Exterior information):

Sensor tab - make sure the camera that is loaded is the Linhoff camera (click New and then Load and navigate to where the *.cam file is saved). If first time, then create a new camera file by selecting New and adding the Focal length (150mm) and the x and y coordinates of the fiducial marks.

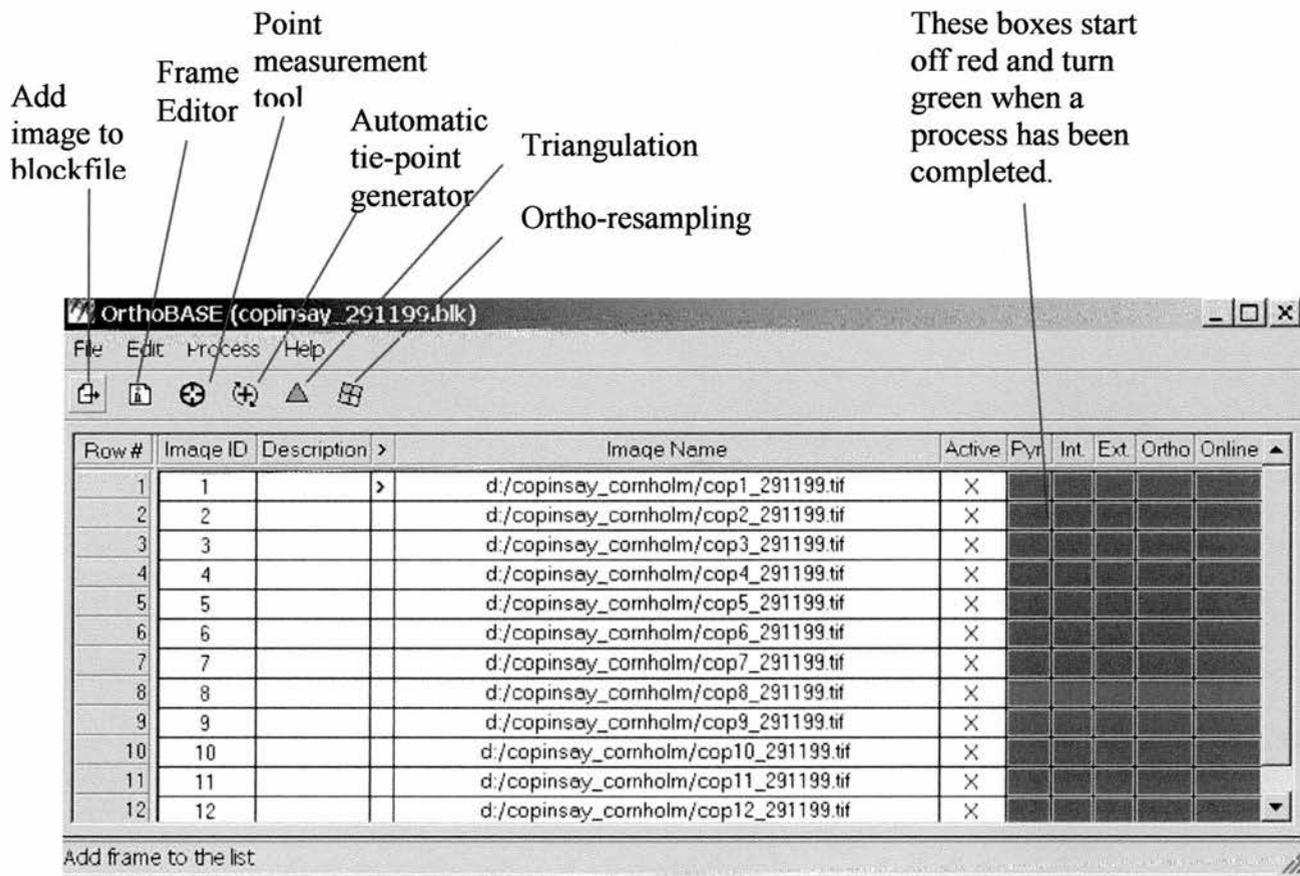


Figure II: A screenshot of the main Orthobase window.

Interior Orientation tab – click Icon 1 (Figure III) to “open viewer for image fiducial measurement”. In the viewer there are 3 versions of the same image at different scales. The scale of the viewers and the area of interested can be adjusted by moving the white boxes (Figure III) by either clicking and dragging the centre of the box to move position or clicking and dragging on a corner of the box to change the scale. Once the first fiducial mark has been located (top left-hand corner), click on Icon 2 (Figure III) and place a cross-hair on the centre of the fiducial mark. ERDAS will automatically navigate to the approximate location of the second fiducial mark. Again, place a cross-hair on top of the fiducial mark. Repeat for all 9 fiducial marks (these must be identified in the correct order, i.e. (1,2,3 along the top, 4,5,6 along the middle, 7,8 and 9 along the bottom). Once all marks have been located on the first image click “Next” and repeat for all images.

Exterior Information tab - click on “Set Status” and set it to initial for each picture (click “Next” until they are all done), then click on “Edit all images”. Enter the x and y co-ordinate of the approximate centre-point for each image (work it out from the GCP positions), then enter a z coordinate which equals 363m for each image as this is the camera height. Enter a kappa value for each image – this is the angle that the plane is flying in relation to North (Check the aerial survey flight record book to find out the angle of flight for each run). Close the frame editor.

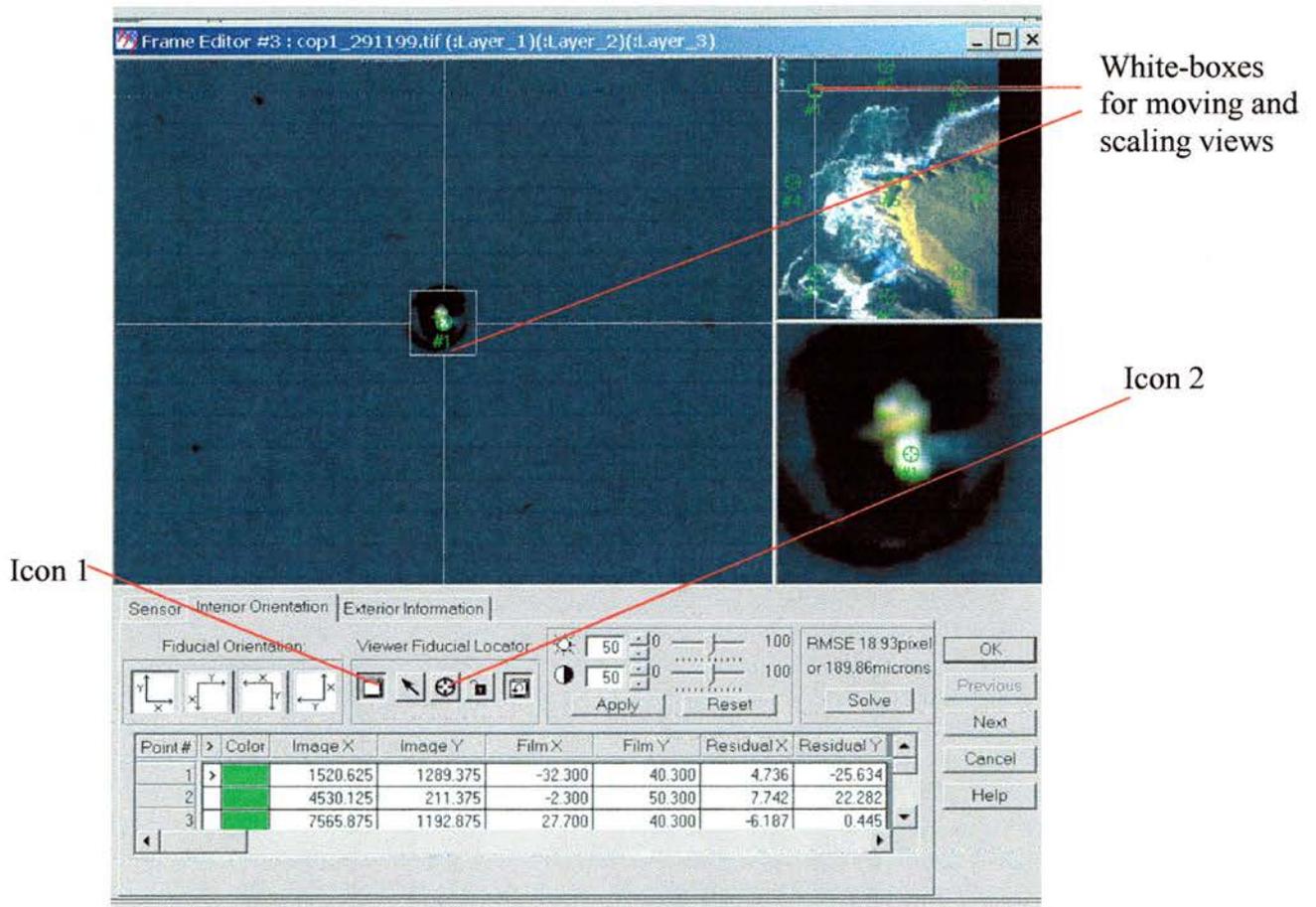


Figure III: A screenshot of the Interior Orientation tab within the Frame Editor.

Locating Ground Control Points and Tie-Points:

Click on the Point measurement tool (Figure II). Choose photos for left and right view from drop-down menus (Figure IV) and match them with the laminated photocopies of the photographs. Find the GCP's on the image using the photocopies and descriptions of the points (the end of the line is exactly where the GPS reading was taken). When the point is located on the screen, click on "Add" and then mark the point using the crosshair (Figure IV). A new point will appear in the table. Change "Type" to "Full" and "Usage" to "Control" by clicking on the box and selecting from the drop-down menu. Enter the x, y and z (altitude) coordinates in the table. (Note - the x coordinate needs a prefix of 3 and the y coordinate needs a prefix of 10 for the islands surveyed so far in Orkney, but check on an OS map that this applies to new islands that are being studied). If a point is present on 2 or more photos then mark the point on all the relevant photos but do not click "Add" if there is already a line in the table for a given GCP. If a GCP or tie-point position is selected in the left hand table then the images in which it has been pinpointed are shown in the right hand table (Figure IV).

If you are unsure of the location of a GCP in the images then leave it out as some points may be covered by the tide.

Tie-points also needed to be added to the overlaps of all the photos. Tie-points have no GPS coordinates associated with them, they are just common points that are present in 2 or more photographs (Figure IV). Do NOT use the "Automatic tie-point

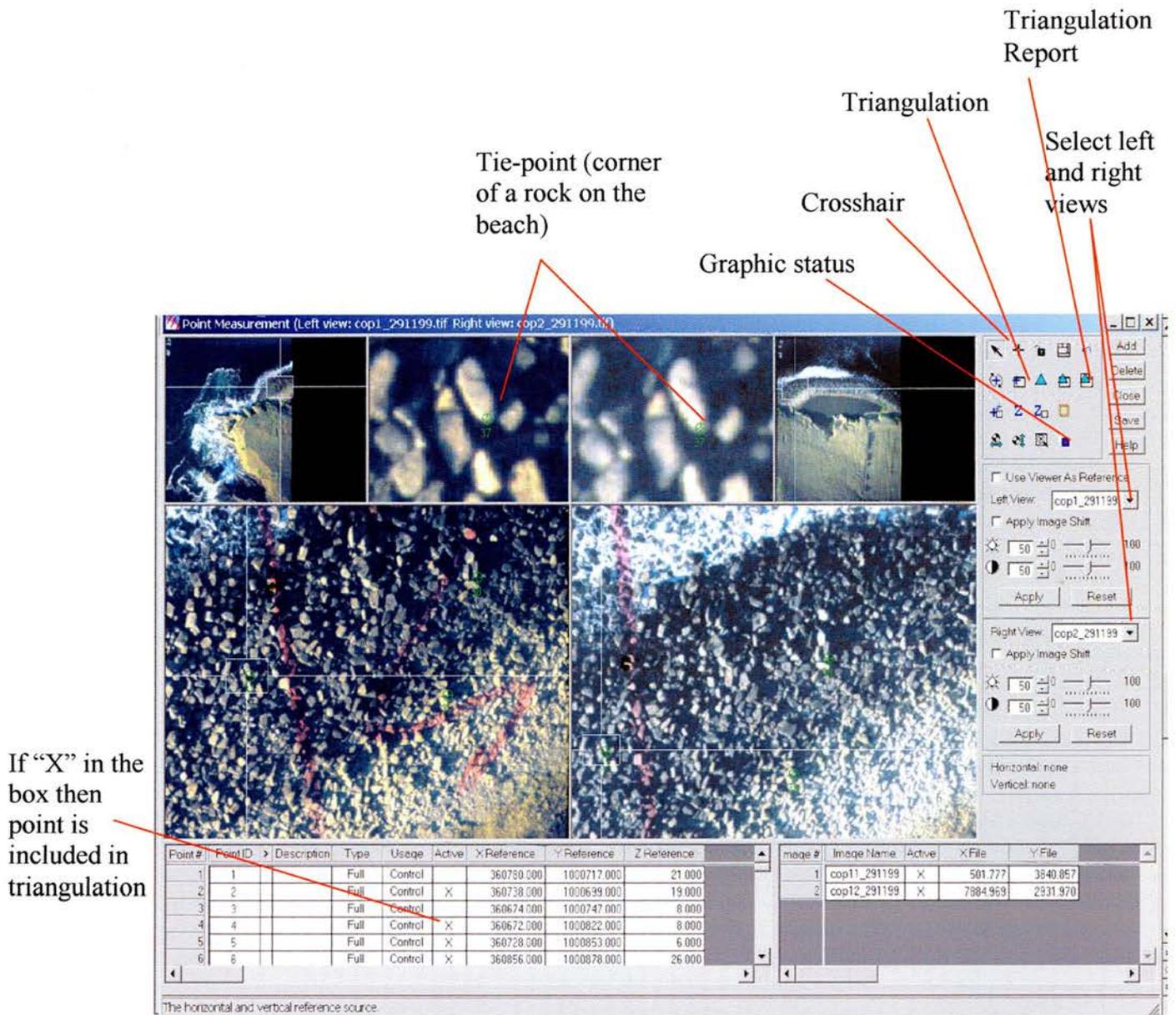


Figure IV: Screenshot of the point measurement tool with different images in the left and right hand viewers. A tie-point can be seen in the high-resolution viewers on both the left and right side.

generator” (Figure II). If it is selected by accident, cancel the process as soon as possible. Tie-points are added to the images as for the GCP’s. In the left-hand table “Type” should be “None” and “Usage” should be “Tie-point”. These are the default settings. 15-20 tie-points should be added to each area of overlap. Note – Try not to use shadows or animals because they change position between photographs.

Triangulation:

Once enough points have been added to the images then triangulation can be performed. Click on the blue triangle (Figure II or Figure IV) and a dialogue box will appear. If triangulation is successful then the dialogue box should state the following:

Triangulation Iteration Convergence: Yes
Total Image Unit-Weight RMSE: less than 2
List of control point RMSE values: less than 2

For accurate rectification the total image unit weight RMSE needs to be as low as possible (always less than 2).

If there is no convergence and/or the error is large, first check for typing errors in the GCP values and then start eliminating each point in turn by removing the “X” in the active box (Figure IV) and clicking “Triangulation” again to see if the error is reduced. Often high error values are due to one or two points.

The Triangulation Report (Figure IV and Table I) is useful for pinpointing the cause of error. If, after checking for typing errors, there is still no improvement check the

Table I: Triangulation report for Copinsay 29 November 1999. This triangulation report is from an accepted triangulation.

The Triangulation Report With OrthoBASE

The output image x, y units: pixels
 The output angle unit: degrees
 The output ground X, Y, Z units: meters

The Input Image Coordinates

image ID = 1

Point ID	x	y
2	5708.959	7431.328
37	7841.630	3280.575
38	8915.033	2859.917
39	8775.418	3364.888
40	7579.625	4373.923
41	8650.480	4341.924
42	8376.977	5142.896
43	7917.883	5538.942
45	8254.433	9138.877
46	7956.955	9407.940
47	8372.537	9753.370
48	8342.345	10620.054

Affine coefficients from file (pixels) to film (millimeters)

A0	A1	A2	B0	B1	B2
-47.4057	0.009942	-0.000047	53.1788	-0.000117	-0.010051

image ID = 2

Point ID	x	y
4	2367.098	4020.126
5	4143.999	5812.546
6	6430.860	10825.901
37	579.349	3776.471
38	1614.982	3382.949
39	1453.735	3876.291
40	204.064	4844.737
41	1239.697	4828.421
42	865.372	5610.665
43	379.709	5994.588
45	372.031	9540.120
46	78.329	9796.389
47	422.269	10148.651
48	335.347	11000.318
49	7774.671	5181.394
50	7856.010	4662.260
51	7745.165	4375.182
52	8328.094	4265.932
53	8090.457	4780.281
54	8717.245	10199.688

Affine coefficients from file (pixels) to film (millimeters)

A0	A1	A2	B0	B1	B2
-49.0922	0.010011	0.000077	56.3380	0.000014	-0.010042

image ID = 3

Point ID	x	y
49	47.278	5672.830
50	136.012	5154.395
51	29.451	4879.204
52	603.110	4752.939
53	370.465	5264.957
54	740.311	10576.022

55	7930.431	5776.974
57	8456.368	6221.386
59	8792.411	6910.373
60	8568.714	7442.275
62	8461.339	9315.365
64	8584.621	10396.070

Affine coefficients from file (pixels) to film (millimeters)

A0	A1	A2	B0	B1	B2
-45.7528	0.009965	-0.000297	61.1424	-0.000337	-0.010029

image ID = 4

Point ID	x	y
12	4506.681	7041.113
13	4676.858	5321.994
55	447.211	5636.896
57	714.278	6091.076
59	960.739	6780.176
60	694.495	7295.353
62	400.226	9136.801
64	417.536	10207.545
65	8382.582	5293.994
66	7943.239	6561.741
67	9005.740	6736.489
68	8497.158	7117.308
69	8567.222	7297.826
70	9061.791	8319.112
71	8560.627	9300.009
72	8033.086	9477.230

Affine coefficients from file (pixels) to film (millimeters)

A0	A1	A2	B0	B1	B2
-47.8335	0.009993	0.000116	57.1909	0.000072	-0.010026

image ID = 5

Point ID	x	y
65	811.872	4712.399
66	204.666	5961.645
67	1243.329	6117.603
68	721.425	6496.570
69	781.263	6673.093
70	1188.911	7662.669
71	635.407	8623.073
72	117.058	8801.840
73	8142.871	2872.612
74	7815.256	2417.841
75	7958.120	3430.604
76	7956.624	4889.911
78	8378.484	6435.235
79	8430.095	7192.938
80	8731.530	8136.887
81	6473.815	1916.036
82	7214.392	4017.060
83	6655.189	135.986

Affine coefficients from file (pixels) to film (millimeters)

A0	A1	A2	B0	B1	B2
-47.7131	0.010004	0.000036	56.3535	-0.000057	-0.010045

image ID = 6

Point ID	x	y
18	2532.253	858.282
22	8179.219	6348.156
73	332.915	3130.862
74	29.157	2685.350
75	181.880	3673.407
76	129.566	5102.756

78	506.732	6623.233
79	529.514	7366.595
80	774.428	8296.743
86	4936.447	7890.732
87	4673.991	9622.824
88	8706.930	8940.558

Affine coefficients from file (pixels) to film (millimeters)

A0	A1	A2	B0	B1	B2
-47.9237	0.009951	0.000051	55.1601	0.000091	-0.009978

image ID = 7

Point ID	x	y
18	4863.714	4372.380
73	3081.293	1721.135
74	3592.036	1526.380
75	2606.528	1462.244
76	1203.353	1103.238
81	4407.482	389.623
82	2231.647	635.850
83	6097.290	978.833

Affine coefficients from file (pixels) to film (millimeters)

A0	A1	A2	B0	B1	B2
-48.3482	0.010031	0.000105	55.7829	0.000066	-0.010031

image ID = 8

Point ID	x	y
22	5259.387	8090.956
86	4491.474	4689.001
87	2904.475	4077.572
88	2698.655	8009.260
90	1193.565	8905.657
91	926.169	8996.227
94	824.817	4975.215
95	3176.038	5467.598

Affine coefficients from file (pixels) to film (millimeters)

A0	A1	A2	B0	B1	B2
-46.2697	0.010001	-0.000166	56.7472	-0.000207	-0.010026

image ID = 9

Point ID	x	y
22	5179.515	3194.403
88	2672.603	3278.867
90	1252.761	4266.273
91	996.292	4374.560
94	667.157	385.753
95	2993.902	761.196
96	633.674	5178.876
97	835.287	5580.677
98	947.136	5882.028

Affine coefficients from file (pixels) to film (millimeters)

A0	A1	A2	B0	B1	B2
-47.1364	0.009927	0.000102	56.3892	0.000024	-0.010044

image ID = 10

Point ID	x	y
26	3685.643	5381.552
90	8368.366	4076.588
91	8108.486	4187.751
96	7641.302	5006.448
97	7875.645	5412.793
98	8015.349	5713.983
94	7849.357	147.591
100	2086.177	4390.547

102	1893.162	1739.385
103	1252.285	507.505
104	1271.404	222.394
105	1345.383	1547.371

Affine coefficients from file (pixels) to film (millimeters)

A0	A1	A2	B0	B1	B2
-47.8381	0.010006	0.000011	55.2305	-0.000018	-0.010017

image ID = 11

Point ID	x	y
29	4302.605	7125.642
100	9176.372	4800.419
102	9083.735	2113.045
103	8482.247	862.357
104	8514.316	571.390
105	8545.603	1918.285
106	1041.474	3894.826
107	990.633	3229.983
108	1685.981	3878.401
109	1803.307	2897.561
110	1637.487	1145.502
111	960.128	1065.721
112	565.133	4483.017
113	501.777	3840.857

Affine coefficients from file (pixels) to film (millimeters)

A0	A1	A2	B0	B1	B2
-47.8957	0.010053	0.000102	60.2273	0.000056	-0.010051

image ID = 12

Point ID	x	y
33	2326.372	2655.921
34	1444.995	3979.646
106	8420.780	2978.244
107	8395.613	2299.551
108	9054.010	2948.206
109	9213.130	1948.027
110	9088.919	164.427
111	8427.274	92.986
112	7919.878	3585.496
113	7884.969	2931.970

Affine coefficients from file (pixels) to film (millimeters)

A0	A1	A2	B0	B1	B2
-47.5560	0.009999	-0.000026	55.5951	-0.000103	-0.010063

ERROR! The GCP or Check point 35 has no image point!

ERROR! The GCP or Check point 36 has no image point!

THE OUTPUT OF SELF-CALIBRATING BUNDLE BLOCK ADJUSTMENT

the no. of iteration =1 the standard error = 2.8280
the maximal correction of the object points = 110.40696

the no. of iteration =2 the standard error = 2.0309
the maximal correction of the object points = 49.97789

the no. of iteration =3 the standard error = 1.7124
the maximal correction of the object points = 6.66622

the no. of iteration =4 the standard error = 1.7035
the maximal correction of the object points = 0.99595

the no. of iteration =5 the standard error = 1.7038
 the maximal correction of the object points = 0.02400

the no. of iteration =6 the standard error = 1.7038
 the maximal correction of the object points = 0.00200

the no. of iteration =7 the standard error = 1.7038
 the maximal correction of the object points = 0.00007

Total Image Unit-
Weight RMSE

* The exterior orientation parameters

image ID	Xs	Ys	Zs	OMEGA	PHI	KAPPA
1	360666.6153	1000747.8671	395.0398	-8.2814	-1.6372	73.3705
2	360725.3666	1000940.2059	370.3700	-10.6144	-0.4359	73.8774
3	360781.2377	1000970.0717	369.7776	12.2815	0.9593	75.2899
4	360862.2558	1001266.4941	389.2037	-4.1904	5.4255	74.9936
5	360912.4273	1001445.1609	376.0488	-5.1811	4.2374	74.9231
6	360957.4807	1001618.3130	371.8129	-2.5893	4.1040	74.7986
7	360818.4728	1001643.4910	370.0287	-5.5581	2.3176	177.9237
8	360994.6156	1001633.4776	377.0067	-3.2200	2.0936	179.2396
9	361001.3707	1001754.8007	380.9338	-3.0805	2.1264	174.4057
10	361152.3234	1001736.8434	377.5787	-2.8824	-1.6479	174.0429
11	361309.5533	1001717.0101	383.8960	-2.0645	-4.4518	174.4037
12	361494.0927	1001702.4640	390.1589	-1.2823	-2.2404	173.8282

Estimated Kappa
angle (angle of
flight in relation
to North)

Estimated
centre
point for
each
image

The interior orientation parameters of photos

image ID	f(mm)	xo(mm)	yo(mm)
1	150.0000	0.0000	0.0000
2	150.0000	0.0000	0.0000
3	150.0000	0.0000	0.0000
4	150.0000	0.0000	0.0000
5	150.0000	0.0000	0.0000
6	150.0000	0.0000	0.0000
7	150.0000	0.0000	0.0000
8	150.0000	0.0000	0.0000
9	150.0000	0.0000	0.0000
10	150.0000	0.0000	0.0000
11	150.0000	0.0000	0.0000
12	150.0000	0.0000	0.0000

Estimated
height of the
camera
(approx 363m)

The residuals of the control points

Point ID	rX	rY	rZ
2	0.0625	-0.0625	0.0000
4	0.0078	-0.0156	0.0313
5	-0.0215	0.0000	-0.5000
6	0.0000	-0.0078	0.0156
12	-0.0112	-0.0039	-0.0313
13	0.0078	-0.0039	-0.1875
18	0.0008	0.0020	0.0103
22	0.0005	0.0002	-0.0054
26	0.0000	0.0000	0.0000
29	0.0039	-0.0068	-0.0625
33	-0.2500	0.2500	0.0000
34	0.0000	-0.0039	-0.0313

aX	aY	aZ
-0.0166	0.0123	-0.0634
mX	mY	mZ
0.0748	0.0746	0.1561

The coordinates of object points

Point ID	X	Y	Z	Overlap
2	360738.0000	1000699.0000	19.0000	1
4	360672.0000	1000822.0000	8.0000	1
5	360728.0000	1000853.0000	6.0000	1
6	360856.0000	1000878.0000	26.0000	1
12	360857.0000	1001226.0000	17.0000	1
13	360815.0000	1001240.0000	6.0000	1

Estimated coordinates of
the GCP's and tie-points.

18	360800.0000	1001577.0000	1.0000	2
22	360970.0000	1001675.0000	10.0000	3
26	361190.0000	1001712.0000	3.0000	1
29	361350.0000	1001730.0000	20.0000	1
33	361558.0000	1001621.0000	39.0000	1
34	361582.0000	1001650.0000	40.0000	1
37	360652.9221	1000779.4220	11.9693	2
38	360650.7965	1000807.5159	8.2060	2
39	360661.8589	1000800.5646	10.2330	2
40	360677.0891	1000765.2815	19.3835	2
41	360684.0674	1000790.3584	15.6972	2
42	360700.6727	1000778.0395	22.2280	2
43	360706.5337	1000764.6776	25.9287	2
45	360789.1498	1000747.4796	41.6449	2
46	360793.1631	1000739.0841	43.0328	2
47	360803.0760	1000745.9829	44.3404	2
48	360821.6611	1000739.5778	47.3712	2
49	360737.4037	1000942.8698	1.3532	2
50	360725.8300	1000948.0493	0.2726	2

The residuals of image points

Point	Image	Vx	Vy
2	1	-0.003	-0.551

Residuals associated with each GCP and tie-point.

Point	Image	Vx	Vy
4	2	1.214	-0.898

Point	Image	Vx	Vy
5	2	-2.519	1.780

Point	Image	Vx	Vy
6	2	1.228	-0.335

Point	Image	Vx	Vy
12	4	0.179	0.442

Point	Image	Vx	Vy
13	4	-0.189	-0.534

Point	Image	Vx	Vy
18	6	-0.152	0.153
18	7	-0.014	0.148

Point	Image	Vx	Vy
22	6	0.020	-0.164
22	8	-0.008	0.023
22	9	-0.074	-0.095

Point	Image	Vx	Vy
26	10	-0.030	-0.058

Point	Image	Vx	Vy
29	11	-0.003	0.101

Point	Image	Vx	Vy
33	12	0.056	0.128

Point	Image	Vx	Vy
34	12	-0.057	-0.144

Point	Image	Vx	Vy
37	1	-0.000	-0.201
37	2	-0.003	0.206

Triangulation Report. Go to * in the Triangulation Report (Table I). This part of the report gives the estimated exterior orientation parameters based on the values that were entered into the Exterior Information in the Frame Editor. Check that the z value is close to 363m. If it is not or is a negative number then this is usually due to the Kappa value that has been entered being wrong. Check whether the estimated Kappa values are similar to what was entered in the Frame Editor. The estimated Kappa may give an indication of what Kappa should be, for example it may be 180° different from the value entered. Change the Kappa value in the Frame Editor (Exterior Information tab) and try triangulation again. To update the Triangulation Report after making a change, the Triangulation result (after clicking the blue triangle) needs to be accepted. If the triangulation result is accepted then x, y and z values will be estimated for the tie-points. These coordinates can be checked for anomalies in the Triangulation Report (Table I, go to #). In particular, check the z value is not out-with what would be expected for a given island. Slight negative values are expected for points close to the shoreline. The residuals of the coordinates can be assessed in the following section of the Triangulation Report (Table I). The residuals should ideally be as low as possible (less than 1). Try eliminating any point with large residuals.

Another way of detecting where any problems lie is to select “Graphic status”. This shows how the photos have been fitted together. Any points with long green lines (residuals) could be eliminated to see if this improves the triangulation result.

If none of the above improve the triangulation results sufficiently then varying the “Triangulation Properties” may help. The following are suggestions of parameters that could be varied:

- Number of iterations – try increasing
- Image point standard deviations – try increasing
- GCP Type and standard deviations – change type to same weighted values and vary the values.
- Change the GCP type back to fixed values and go to advanced options tab – choose a blunder checking model, it doesn’t matter which one. This will automatically miss out points that are too bad to be included.

Only vary one parameter at a time and rerun triangulation after each change.

Ortho-resampling:

Once the RMSE is as low as possible then the images can be ortho-resampled (Figure II). In the dialogue box select “Multiple output”. Navigate to where the files should be saved. Only enter “ortho” as the file name and this will be put as a prefix in front of each image file (eg orthocopinsay_291199.img). If a DEM file is available (see Appendix 1) select “DEM file” and navigate to where this is saved. If a DEM is not available for a set of photographs select “Constant value” and use the mean of the GCP z values for the island. Leave the other options as the default values.

Once the ortho-resampling is completed all the boxes on the main Orthobase menu should be green (Figure II)

Viewing the Ortho-rectified images:

To view the rectified images open the Viewer, which can be found in the main ERDAS menu. In the Viewer select “Open” and “Raster file”. Navigate to, and select the image you wish to view. Before clicking “OK”, select the Raster tab and make the following options:

- deselect “Clear viewer”
- select “Fit to frame”
- select “Background transparent”

Open all images that make up an island. All images in the viewer can be saved as one file by selecting “File – Save – View” and this will save the whole view as a *.vue file. There are a number of ways to check how accurate the overlap is between 2 images. An image can be scrolled back so that the underlying image can be viewed using “Utility – Swipe”. The image that will scroll will be the uppermost image. To change the image that is on top of all other images, select “View – Arrange Layers”, drag the image labels to the desired position and click “Apply” before closing the dialogue box. If, by scrolling, the same object can be seen in both images, the distance between the position of an object in one image and its position in another image (ie the overlap error) can be measured using the Measurement Tool (Figure V). In the Measurement Tool dialogue box select the line and click the start and end of the line on the object in both images. The measurement will appear in the dialogue box.

Measurement Tool

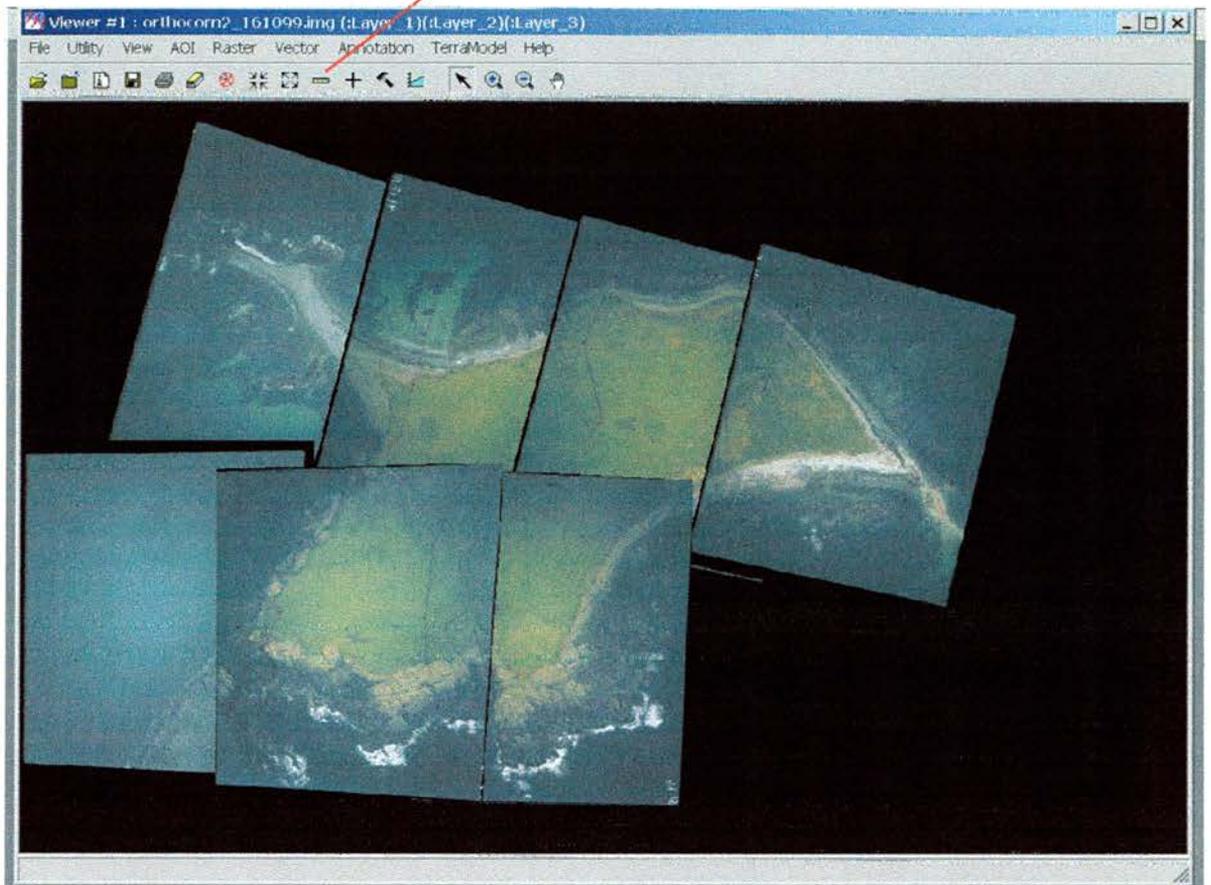


Figure V: Screenshot of the Viewer showing all Orthocornholm images from the 16 October 1999.

Creating vector layers of topography and pup distributions:

Vector layers can be created for each of the topographical and distributional parameters that are extracted. Polygon vector layers should be created for the coastline and pools of water. Point vector layers should be created for pinpointing animals. Click “File-New-Vector layer” and navigate to a directory to save the vector file. Click “File of Type” and select “shapefile” as this format is compatible with Arcview. This vector layer will be on top of all the images (you can check in “View-Arrange layers”). To start editing the vector layer, click “Vector – Enable editing”. Click “Vector-Tools” to show the vector toolbar (Figure VI). Draw polygons around pools of water and the coastline using the polygon tool (Figure VI) and pinpoint animals using the crosshair (Figure VI). To select a polygon or point to move or delete it, use the “select” tool to click on the object, which will turn yellow when selected. To delete a polygon or point go to “Vector-Delete”. To change the appearance of the polygons or points select “Vector-Viewing properties” where different colours and sizes can be chosen. Once finished, these vector layers can be opened in Arcview.

Vector Toolbar

Select

Crosshair

Polygon tool

Point vector pinpointing
pup positions

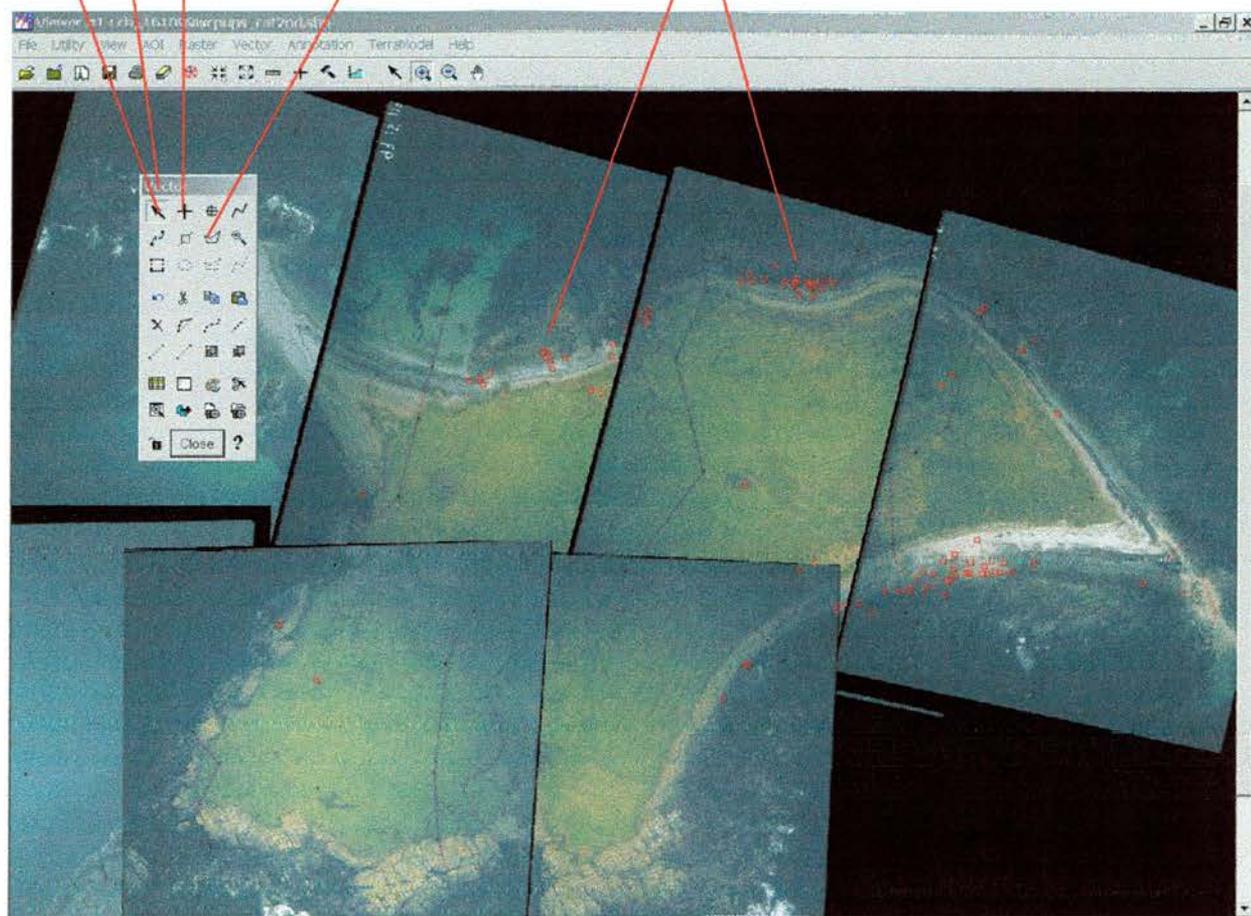


Figure VI: Screenshot of Viewer with point vector layer overlaying the images and the vector toolbar.

Appendix 3

Codes and Formulas for Models.

Pathdistance Model in Arcinfo Grid:

Distance = pathdistance(source, cost, surface, #,#, surface, "cos_sec lcutangle=-84 hcutangle=84 cospower=2 secpower=2")

Where:

Source = either the coastline grid (for calculating the distance to access surface) or the combined coastline and pools of water grid (for calculating the distance to water surface) where cells containing water have a value of 1 and cells for which a value is to be calculated have "No Data".

Cost = a grid including any barriers to movement such as cliffs where all cells in the grid have a value of 1 with the exception of cells which represent a barrier and therefore have "No Data".

Surface = this is a grid interpolated from an OS Land-Form Panorama DEM.

Model Fitted to the Presence/Absence of Aggression:

The following code was written in R:

```
agg <- read.table("agg.csv", header=T, sep=",")

{
aggmod <- glm(agg$prop~V+V2+V3+V4+V5+day+I(day^2)+I(day^3)+I(day^4)
+V:V2+V:V4+V:V5+V:day+V:I(day^2)+V:I(day^3)+V:I(day^4)+V2:V3+V2:V5+V
2:day+V2:I(day^2)+V2:I(day^3)+V2:I(day^4)+V3:I(day^4)+V4:V5+V4:day+V4:I(da
y^2)+V4:I(day^3)+V5:I(day^2)+V5:I(day^3)+V5:I(day^4)+V:V2:V3+V:V2:V4+V:V
2:V5+V:V2:day+V:V2:I(day^2)+V:V2:I(day^3)+V:V2:I(day^4)+V:V3:day+V:V3:I(
day^4)+V:V4:V5+V:V4:day+V:V4:I(day^2)+V:V4:I(day^3)+V:V4:I(day^4)+V:V5:d
ay+V:V5:I(day^2)+V:V5:I(day^3)+V:V5:I(day^4)+V2:V3:V4+V2:V3:day+V2:V3:I(
day^2)+V2:V3:I(day^3)+V2:V3:I(day^4)+V2:V4:V5+V2:V4:day+V2:V5:day+V2:V
5:I(day^2)+V2:V5:I(day^4)+V3:V4:day+V3:V4:I(day^2)+V3:V5:I(day^2)+V3:V5:I(
day^3)+V3:V5:I(day^4)+V4:V5:day+V4:V5:I(day^2)+V4:V5:I(day^3)+V4:V5:I(day
^4), data=agg, family = binomial(link = probit), weights = agg$Freq)
}
```

Where:

agg = a table containing the response and explanatory variables

prop = the proportion of cells in each habitat type that contained an aggressive

interaction (response variable)

V = distance to water

V2 = distance to access

V3 = slope

V4 = mean number of neighbouring pups

V5 = pup presence

Day = day of the breeding season

Freq = the number of cells in each habitat type

Model Fitted to the Presence/Absence of Newborn Pups:

The following code was written in R:

```
newpups <- read.table("newpuphab.csv", header=T, sep=",")
{
newbornmod <- glm(newpups$propocc ~ V+V2 + I(V2^2)+ V3 + V4 + V5 + V6 +
day + I(day^2) + I(day^3) + I(day^4) + V:V2 +V:V3 + V:V4 + V:V5 + V:V6 + V:day
+ V:I(day^3) + V:I(day^4) + V2:V3 + V2:V4 + V2:V5 + V2:V6 + V2:day +
V2:I(day^2) +V2:I(day^3) +V2:I(day^4)+ V3:V4 + V3:V5 + V3:V6 + V3:day +
V3:I(day^2) + V3:I(day^3) + V4:V5 + V4:V6 + V4:I(day^2) + V4:I(day^3) + V5:day
+ V5:I(day^2) + V5:I(day^3) + V5:I(day^4) + V6:day + V6:I(day^2) + V6:I(day^3) +
V6:I(day^4) + V:V2:V6 + V:V2:day + V:V2:I(day^3) + V:V2:I(day^4)+ V:V3:V4 +
V:V3:day + V:V4:V6 + V:V4:I(day^3) + V2:V3:I(day^2) + V2:V3:I(day^3) +
V2:V4:V6 + V2:V5:day + V2:V6:I(day^2) + V3:V4:V6 + V3:V6:I(day^3) +
V4:V6:I(day^2) , family=quasibinomial(link=probit), data=newpups,
weights=newpups$Freq, control=glm.control(epsilon=.001, maxit=5000,
trace=FALSE))
}
```

Where:

Newpups = a table containing the response and explanatory variables

Propocc = the proportion of cells in each habitat type that are occupied by newborn
pups (response variable)

V = distance to water

V2 = distance to access

V3 = slope

V4 = mean number of neighbouring pups

V5 = pup presence

V6 = probability of aggression occurring

Day = day of the breeding season

Freq = the number of cells in each habitat type

Code for Simulation of Newborn Pup Arrival and Evaluation of Models:

The following code was written in R:

```
##-----aggression model-----

agg <- read.table("agg.csv", header=T, sep=",")
{
aggmod <- glm(agg$propused ~
V+V2+V3+V4+V5+day+I(day^2)+I(day^3)+I(day^4)
+V:V2+V:V4+V:V5+V:day+V:I(day^2)+V:I(day^3)+V:I(day^4)+V2:V3+V2:V5+V
2:day+V2:I(day^2)+V2:I(day^3)+V2:I(day^4)+V3:I(day^4)+V4:V5+V4:day+V4:I(da
y^2)+V4:I(day^3)+V5:I(day^2)+V5:I(day^3)+V5:I(day^4)+V:V2:V3+V:V2:V4+V:V
2:V5+V:V2:day+V:V2:I(day^2)+V:V2:I(day^3)+V:V2:I(day^4)+V:V3:day+V:V3:I(
day^4)+V:V4:V5+V:V4:day+V:V4:I(day^2)+V:V4:I(day^3)+V:V4:I(day^4)+V:V5:d
ay+V:V5:I(day^2)+V:V5:I(day^3)+V:V5:I(day^4)+V2:V3:V4+V2:V3:day+V2:V3:I(
day^2)+V2:V3:I(day^3)+V2:V3:I(day^4)+V2:V4:V5+V2:V4:day+V2:V5:day+V2:V
5:I(day^2)+V2:V5:I(day^4)+V3:V4:day+V3:V4:I(day^2)+V3:V5:I(day^2)+V3:V5:I(
day^3)+V3:V5:I(day^4)+V4:V5:day+V4:V5:I(day^2)+V4:V5:I(day^3)
+V4:V5:I(day^4), data=agg, family = binomial(link = probit), weights = agg$Freq)
}

rm(agg)

#-----newborn pup model-----
newpups <- read.table("newpuphab.csv", header=T, sep=",")
{
newbornmod <- glm(newpups$propocc ~ V+V2 + I(V2^2)+ V3 + V4 + V5 + V6 +
day + I(day^2) + I(day^3) + I(day^4) + V:V2 +V:V3 + V:V4 + V:V5 +
V:V6 + V:day + V:I(day^3) + V:I(day^4) + V2:V3 + V2:V4 +
V2:V5 + V2:V6 + V2:day + V2:I(day^2) +V2:I(day^3) +V2:I(day^4)+
V3:V4 + V3:V5 + V3:V6 + V3:day + V3:I(day^2) + V3:I(day^3) +
V4:V5 + V4:V6 + V4:I(day^2) + V4:I(day^3) + V5:day + V5:I(day^2) +
V5:I(day^3) + V5:I(day^4) + V6:day + V6:I(day^2) + V6:I(day^3) +
V6:I(day^4) + V:V2:V6 + V:V2:day + V:V2:I(day^3) + V:V2:I(day^4)+
V:V3:V4 + V:V3:day + V:V4:V6 + V:V4:I(day^3) + V2:V3:I(day^2) +
V2:V3:I(day^3) + V2:V4:V6 + V2:V5:day + V2:V6:I(day^2) +
V3:V4:V6 + V3:V6:I(day^3) + V4:V6:I(day^2)
, family=quasibinomial(link=probit), data=newpups,
weights=newpups$Freq,control=glm.control(epsilon=.001, maxit=5000,
trace=FALSE))
}

rm(newpups)

survey1 <- rep(0,79344)
survey2 <- rep(0,79344)
```

```
survey3 <- rep(0,79344)

for(m in 1:30){

#-----read in all survey tables-----

chcells161099 <- read.table("ch161099.csv", header=T, sep=",")
chcells111199 <- read.table("ch111199.csv", header=T, sep=",")
chcells291199 <- read.table("ch291199.csv", header=T, sep=",")
#-----convert it to day 0-----

chday <- chcells161099
chday$pups <- rep(0, times=nrow(chday))
chday$autocov <- rep(0, times=nrow(chday))
aggpred <- rep(0, times=nrow(chday))
pupid <- rep(0, times=nrow(chday))
puptm <- rep(0, times=nrow(chday))
chday <- cbind(chday, aggpred, pupid, puptm)

rm(aggpred, pupid, chcells161099)

days <- c(1:55)

for(i in 1:length(days)){

#-----change pool positions-----

day <- rep(i, 79344)
chday$distwater <- ifelse(day>26, chcells111199$distwater, chday$distwater)
chday$distwater <- ifelse(day>50, chcells291199$distwater, chday$distwater)

rm(day)
#-----assign habitat types to each cell-----

Lo <- c(0, 0, -0.5, 0,0); #Habitat Availability
Hi <- c(130, 230, 3.5, 40,1);
bins <- c(13, 23, 4, 4,10);

for(var in 1:5)

{
lev <- Lo[var] + abs(Hi[var]-Lo[var])/bins[var]*((1:bins[var])-1/2);
ordered(cut(chday[, var],
breaks= Lo[var]+abs(Hi[var]-Lo[var])/bins[var]*(0:bins[var]), labels=lev,
include.lowest=T),
levels=lev)-> V;
if (var==1) chhab <- as.data.frame(V) else chhab[, var] <- V
}

chhabitatsday <- as.data.frame(chhab);
```

```
V <- chhabitatsday$V
V2 <- chhabitatsday$V2
V3 <- chhabitatsday$V4
V4 <- chhabitatsday$V5
V5 <- chhabitatsday$V3
day <- rep(i, 79344)

chhabitatsday <- data.frame(V)
chhabitatsday <- cbind(chhabitatsday, V2, V3, V4, V5,day)

rm(V, V2, V3, V4, V5, Lo, Hi, bins, chhab, lev, var)

chhabitatsday$V <- as.numeric(as.character(chhabitatsday$V))
chhabitatsday$V2 <- as.numeric(as.character(chhabitatsday$V2))
chhabitatsday$V3 <- as.numeric(as.character(chhabitatsday$V3))
chhabitatsday$V4 <- as.numeric(as.character(chhabitatsday$V4))
chhabitatsday$V5 <- as.numeric(as.character(chhabitatsday$V5))

chhabitatsday$V[is.na(chhabitatsday$V)] <- 1000
chhabitatsday$V2[is.na(chhabitatsday$V2)] <- 1000

#-----predict aggression using aggmod-----

chaggpred <- predict.glm(aggmod, newdata=chhabitatsday, type="response")

rm(chhabitatsday, day)
#-----add predicted aggression to chday-----

chday$aggpred <- chaggpred

rm(chaggpred)

#-----assign habitat types to cells for newbornmod-----

Lo <- c(0, 0, -0.5, 0,0,0); #Habitat Availability
Hi <- c(130, 230, 1.5, 40,1,1);
bins <- c(13, 23, 2, 4,10,4);

for(var in 1:6)
{
lev <- Lo[var] + abs(Hi[var]-Lo[var])/bins[var]*((1:bins[var])-1/2);
ordered(cut(chday[, var],
breaks= Lo[var]+abs(Hi[var]-Lo[var])/bins[var]*(0:bins[var]), labels=lev,
include.lowest=T),
levels=lev)-> V;
if (var==1) chpuphab <- as.data.frame(V) else chpuphab[, var] <- V
}

chnewpuphabday <- as.data.frame(chpuphab);
```

```
V <- chnewpuphabday$V
V2 <- chnewpuphabday$V2
V3 <- chnewpuphabday$V4
V4 <- chnewpuphabday$V5
V5 <- chnewpuphabday$V3
V6 <- chnewpuphabday$V6
day <- rep(i, 79344)
newpuphab <- data.frame(V)
newpuphab <- cbind(newpuphab, V2, V3, V4, V5, V6, day)

rm(chnewpuphabday,V, V2, V3, V4, V5, V6, day, Lo, Hi, bins, chpuphab, lev, var)

newpuphab$V <- as.numeric(as.character(newpuphab$V))
newpuphab$V2 <- as.numeric(as.character(newpuphab$V2))
newpuphab$V3 <- as.numeric(as.character(newpuphab$V3))
newpuphab$V4 <- as.numeric(as.character(newpuphab$V4))
newpuphab$V5 <- as.numeric(as.character(newpuphab$V5))
newpuphab$V6 <- as.numeric(as.character(newpuphab$V6))

newpuphab$V[is.na(newpuphab$V)] <- 1000
newpuphab$V2[is.na(newpuphab$V2)] <- 1000

#-----new born pup predictions-----

chpuppredday <- predict.glm(newbornmod, newdata=newpuphab, type="response")

#-----choose positions of pups-----

pupsborn <- read.table("ch99tmpupprod.csv", header=T, sep=",")

cellid <- c(1:79344)

tm <-
c(16,19,15,15,13,14,16,16,15,13,12,17,17,15,17,13,11,13,17,15,15,18,15,16,16,11,17,
19,14,14,13,14,17,14,16,15)
p <- sample(tm,1,replace=TRUE)

chday$pups <- ifelse(chday$pupid[cellid]==(i-chday$puptm[cellid]), 0,
chday$pups[cellid])

land <- rep(0,79344)
land <- ifelse(newpuphab$V==1000,0,1)
chpuppredday <- chpuppredday*land

samp <- pupsborn[3]
x <- sample(cellid, samp$X1[i+1], replace=FALSE, chpuppredday)

chday$pups[x] <- 1
chday$pupid[x] <- i
chday$puptm[x] <- p
```

```
day <- rep(i, 79344)

pups1 <- rep(0, times=nrow(chday))
pups2 <- rep(0, times=nrow(chday))
pups3 <- rep(0, times=nrow(chday))

pups1 <- ifelse(day==11, chday$pups, 0)
pups2 <- ifelse(day==37, chday$pups, 0)
pups3 <- ifelse(day==55, chday$pups, 0)

survey1 <- survey1 + pups1
survey2 <- survey2 + pups2
survey3 <- survey3 + pups3

rm(x, pupsborn, samp, newpuphab, pups1, pups2, pups3)

#-----make autocov surface-----
puppres <- matrix(chday$pups, 232, 342, byrow=F)

rm(chpuppredday)

puppres <- ifelse(puppres>0, 1, 0)

pups <- mat.or.vec(dim(puppres)[1], dim(puppres)[2])

for(k in 2:nrow(puppres)-1) {
  for(j in 2:ncol(puppres)-1){
    pups[k,j] <- (sum(puppres[(k-1):(k+1), (j-1):(j+1)])-puppres[k,j])/8
  }
}

chday$autocov <- as.vector(pups)

rm(pups, puppres, k, j, cellid)

}
}

##-----

probability1 <- survey1/30
probability2 <- survey2/30
probability3 <- survey3/30

write.table(probability1, file="probability1.csv", sep=",")
write.table(probability2, file="probability2.csv", sep=",")
write.table(probability3, file="probability3.csv", sep=",")
```

```
##-----make prob distribution from 30 realisations under a random model-----

probability1 <- read.csv("probability1.csv")
probability2 <- read.csv("probability2.csv")
probability3 <- read.csv("probability3.csv")

randsurv1 <- rep(0,79344)
randsurv2 <- rep(0,79344)
randsurv3 <- rep(0,79344)

chcells161099 <- read.table("ch161099.csv", header=T, sep=",")

for(j in 1:30){
  rand1 <- rep(0,79344)
  cellid <- c(1:79344)
  land <- rep(0, 79344)
  land <- ifelse(chcells161099$distwater== -1, 0,1)
  z <- sample(cellid, 98, replace=FALSE,land)
  rand1[z] <-1
  randsurv1 <- randsurv1 + rand1
}
randsurv1 <- randsurv1/30

chcells111199 <- read.table("ch111199.csv", header=T, sep=",")

for(j in 1:30){
  rand2 <- rep(0,79344)
  cellid <- c(1:79344)
  land <- rep(0, 79344)
  land <- ifelse(chcells111199$distwater== -1, 0,1)
  z <- sample(cellid, 620, replace=FALSE,land)
  rand2[z] <-1
  randsurv2 <- randsurv2 + rand2
}
randsurv2 <- randsurv2/30

chcells291199 <- read.table("ch291199.csv", header=T, sep=",")

for(j in 1:30){
  rand3 <- rep(0,79344)
  cellid <- c(1:79344)
  land <- rep(0, 79344)
  land <- ifelse(chcells291199$distwater== -1, 0,1)
  z <- sample(cellid, 246, replace=FALSE,land)
  rand3[z] <-1
  randsurv3 <- randsurv3 + rand3
}
randsurv3 <- randsurv3/30

randsurv1 <- data.frame(randsurv1)
```

```
randsurv2 <- data.frame(randsurv2)
randsurv3 <- data.frame(randsurv3)

write.table(randsurv1, file="randsurv1.csv", sep=",")
write.table(randsurv2, file="randsurv2.csv", sep=",")
write.table(randsurv3, file="randsurv3.csv", sep=",")
##-----replacing zero's-----

replprob <- read.csv("replaceprobability.csv")
survey1aic <- data.frame(c(0))
survey2aic <- data.frame(c(0))
survey3aic <- data.frame(c(0))

random1aic <- data.frame(c(0))
random2aic <- data.frame(c(0))
random3aic <- data.frame(c(0))

for(m in 1:200){

probability1 <- read.csv("noaccprobability1.csv")
probability2 <- read.csv("noaccprobability2.csv")
probability3 <- read.csv("noaccprobability3.csv")

randsurv1 <- read.csv("randsurv1.csv")
randsurv2 <- read.csv("randsurv2.csv")
randsurv3 <- read.csv("randsurv3.csv")

probability1$x <- ifelse(probability1$x==0, replprob$replprob[m], probability1$x)
probability2$x <- ifelse(probability2$x==0, replprob$replprob [m], probability2$x)
probability3$x <- ifelse(probability3$x==0, replprob$replprob [m], probability3$x)

randsurv1$randsurv1 <- ifelse(randsurv1$randsurv1==0, replprob$replprob [m],
randsurv1$randsurv1)
randsurv2$randsurv2 <- ifelse(randsurv2$randsurv2==0, replprob$replprob [m],
randsurv2$randsurv2)
randsurv3$randsurv3 <- ifelse(randsurv3$randsurv3==0, replprob$replprob [m],
randsurv3$randsurv3)

y <- sum(probability1)
probability1 <- probability1/y
y <- sum(probability2)
probability2 <- probability2/y
y <- sum(probability3)
probability3 <- probability3/y

z <- sum(randsurv1)
randsurv1 <- randsurv1/z
z <- sum(randsurv2)
randsurv2 <- randsurv2/z
```

```
z <- sum(randsurv3)
randsurv3 <- randsurv3/z

##---survey1-----

chcells161099 <- read.table("ch161099.csv", header=T, sep=",")
actpups <- chcells161099$pups

probactual1 <- data.frame(cbind(probability1, actpups))
probactual1$actpups <- ifelse(probactual1$actpups>1, 1, probactual1$actpups)
probp1 <- subset(probactual1, probactual1$actpups==1)
prodp1 <- sum(log(probp1$x))
aic <- (-2*prodp1) +(2*61)
survey1aic <- rbind(survey1aic, aic)

probrand1 <- data.frame(cbind(randsurv1, actpups))
probrand1$actpups <- ifelse(probrand1$actpups>1, 1, probrand1$actpups)
probp1 <- subset(probrand1, probrand1$actpups==1)
prodp1 <- sum(log(probp1$randsurv1))
aic <- (-2*prodp1) +(2*1)
random1aic <- rbind(random1aic, aic)

rm(probactual1, probrand1,probp1,prodp1)

##---survey2-----

chcells111199 <- read.table("ch111199.csv", header=T, sep=",")
actpups <- chcells111199$pups

probactual2 <- data.frame(cbind(probability2, actpups))
probactual2$actpups <- ifelse(probactual2$actpups>1, 1, probactual2$actpups)
probp2 <- subset(probactual2, probactual2$actpups==1)
prodp2 <- sum(log(probp2$x))
aic <- (-2*prodp2) +(2*61)
survey2aic <- rbind(survey2aic, aic)

probrand2 <- data.frame(cbind(randsurv2, actpups))
probrand2$actpups <- ifelse(probrand2$actpups>1, 1, probrand2$actpups)
probp2 <- subset(probrand2, probrand2$actpups==1)
prodp2 <- sum(log(probp2$randsurv2))
aic <- (-2*prodp2) +(2*1)
random2aic <- rbind(random2aic, aic)

##---survey3-----

chcells291199 <- read.table("ch291199.csv", header=T, sep=",")
actpups <- chcells291199$pups

probactual3 <- data.frame(cbind(probability3, actpups))
probactual3$actpups <- ifelse(probactual3$actpups>1, 1, probactual3$actpups)
```

```
probp3 <- subset(probactual3, probactual3$actpups==1)
prodp3 <- sum(log(probp3$x))
aic <- (-2*prodp3) +(2*61)
survey3aic <- rbind(survey3aic, aic)

probrand3 <- data.frame(cbind(randsurv3, actpups))
probrand3$actpups <- ifelse(probrand3$actpups>1, 1, probrand3$actpups)
probp3 <- subset(probrand3, probrand3$actpups==1)
prodp3 <- sum(log(probp3$randsurv3))
aic <- (-2*prodp3) +(2*1)
random3aic <- rbind(random3aic, aic)

}
```

Model Fitted to the Presence/Absence of Aggression with Distance to Access**Excluded:**

The following code was written in R:

```
agg <- read.table("agg.csv", header=T, sep=",")

{
aggmod <- glm(agg$propused ~ V+V3+V4+V5+day+I(day^2)+I(day^3)+I(day^4)
+V:V4+V:V5+V:day+V:I(day^2)+V:I(day^3)+V:I(day^4)+V3:I(day^4)+V4:V5+V4:
day+V4:I(day^2)
+V4:I(day^3)+V5:I(day^2)+V5:I(day^3)+V5:I(day^4)+V:V3:day+V:V3:I(day^4)+V:
V4:V5+V:V4:day
+V:V4:I(day^2)+V:V4:I(day^3)+V:V4:I(day^4)+V:V5:day+V:V5:I(day^2)+V:V5:I(
day^3)
+V:V5:I(day^4)+V3:V4:day+V3:V4:I(day^2)+V3:V5:I(day^2)+V3:V5:I(day^3)
+V3:V5:I(day^4)+V4:V5:day+V4:V5:I(day^2)+V4:V5:I(day^3)
+V4:V5:I(day^4), data=agg, family = binomial(link = probit), weights = agg$Freq)
}
```

Where:

agg = a table containing the response and explanatory variables

prop = the proportion of cells in each habitat type that contained an aggressive

interaction (response variable)

V = distance to water

V3 = slope

V4 = mean number of neighbouring pups

V5 = pup presence

Day = day of the breeding season

Freq = the number of cells in each habitat type

Model Fitted to the Presence/Absence of Newborn Pups with Distance to Access**Excluded:**

The following code was written in R:

```
newpups <- read.table("noaccnewpuphab.csv", header=T, sep=",")
{
newbornmod <- glm(newpups$propocc~V+V3+V4+V5+V6+day+I(day^2)
+I(day^3)+I(day^4)+V:V3+V:V4+V:V5+V:day+V:I(day^2)+V:I(day^3)+V:I(day^4)
+V3:V4+V3:V6+V3:day+V3:I(day^3)+V4:V5+V4:day+V4:I(day^2)+V4:I(day^4)+V
5:V6+V5:day+V5:I(day^2)+V6:day+V6:I(day^2)+V6:I(day^4)+V:V3:V4+V:V3:V5+
V:V3:day+V:V3:I(day^3)+V:V3:I(day^4)+V:V4:day+V:V4:I(day^4)+V:V5:day
+V:V5:I(day^2)+V3:V4:day+V3:V4:I(day^2)+V3:V5:day+V3:V5:I(day^3)
+V3:V6:day+V4:V6:I(day^3), data=newpups, family=quasibinomial(link=probit),
weights=newpups$Freq,control=glm.control(epsilon=.001, maxit=5000,
trace=FALSE))
}
```

Where:

Newpups = a table containing the response and explanatory variables

Propocc = the proportion of cells in each habitat type that are occupied by newborn
pups (response variable)

V = distance to water

V3 = slope

V4 = mean number of neighbouring pups

V5 = pup presence

V6 = probability of aggression occurring

Day = day of the breeding season

Freq = the number of cells in each habitat type