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# **Sociality of female grey seals breeding on North Rona, Scotland**

Submitted for the degree of  
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I, Simon James Sinclair Ruddell, hereby certify that this thesis, which is approximately 50,000 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 1.08.05  
Signature of candidate

I was admitted as a research student in August 2001 and as a candidate for the degree of PhD in August 2001; the higher study for which this is a record was carried out in the University of St Andrews between 2001 and 2005.

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I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor 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

Social structure has potential consequences for individual fitness. However, traditional methods of analysing social structure have limitations when applied to pinniped breeding colonies. Here, a novel methodology for the quantification and assessment of social structure is presented. The measure of social stability describes change in the social environment through time and may have utility to other studies in providing an alternative view of social structure.

Photo identification and high resolution mapping was used to record the spatio-temporal organisation of females within the North Rona colony during the 2002 and 2003 breeding seasons. Fine-scale observations of seal behaviour suggested that associations were most likely to be present at a scale of 10m within seasons and 20m throughout seasons. Using these scales, social stability was calculated both within areas and around individuals and both within and between years. In addition, the first estimate of mixing between different areas of the North Rona colony is presented.

There was no conclusive evidence that between year social stability or pair-wise re-associations occurred more than would be expected from a model incorporating site fidelity, temporal fidelity and site choice. However, higher values of between year social stability were associated with animals that pupped early in the season in areas of high density, low slope and easy access to the sea.

There were both areas and individuals within the colony that were found to be associated with more extreme values of within year social stability than could be explained by a model incorporating site fidelity, site choice and temporal attendance. Areas of elevated within year social stability were also

those towards the centre of the colony with moderate access to pools and which were well populated with females at different stages of lactation. There was no evidence for reduced aggression in areas of elevated social stability and so the mechanism by which social stability may provide a benefit to breeding females is unclear. However, maternal efficiency, the proportion of maternal expenditure realised as pup mass gain, tended to be higher for mothers with high social stability values. These results provide evidence of social complexity within a grey seal breeding colony and the first indication of a possible fitness benefit of social behaviour for these animals.

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# **Chapter 1**

## **General Introduction**

## 1.1 Introduction

In the broadest sense, sociality is defined as the aggregation of individuals of the same species. In general, animals aggregate for the exploitation of resources, the main examples of which being food and mating opportunity. But these aggregations may also provide other advantages, such as safety in numbers, improved foraging efficiency, resource defence and care of young (Krebs & Davies, 1993). Disadvantages may also be associated with groups of individuals, however, such as increased competition, aggression and risk of infection (Krebs & Davies, 1993).

In order to investigate sociality further, it can be subdivided into three primary categories of analysis: interactions, relationships and social structure (Hinde, 1976). Here, an interaction constitutes a single encounter wherein each participating individual influences the behaviour of the other. Any action in an interaction may produce many different reactions, which could in turn depend upon motivation and relationships. Relationships are built up over a series of interactions and are based on the content, quality and patterning of those component interactions. The social structure of any group, then, is the network of relationships that exist between the individuals within that group.

Female grey seals are social, at least to the extent of aggregating on breeding colonies once a year to raise a pup and mate (Hewer, 1964). However, to gain further insight into female grey seal sociality within both life history and evolutionary contexts it is necessary to describe social behaviour, to understand its function and to assess its impact on reproductive success (Altman 2003). In doing so it is possible to better understand the life history of grey seals, the

variation in behaviour and success between individuals and the evolution of sociality itself.

Social systems vary widely across the animal kingdom from highly developed to loosely organised and temporary aggregations. On first encounter, grey seals appear to be of the latter, but on further investigation life history parameters and individual behaviour illustrate the possibilities for social complexity. Here, I outline some of the degrees of sociality within the animal kingdom, the theory of cooperation, the life history parameters of grey seals and the possibility of sociality within female grey seals breeding on North Rona, Scotland.

### 1.1.1 Degrees of sociality

The most extreme case of Hamilton's (1964) rule of inclusive fitness is evident in the eusocial insects where social structure is based solely on the relatedness of individuals in a group to one another. Here, under the rules of a haplodiploidy system, individuals can increase the propagation of their genes by being altruistic to relatives. An example of a haplodiploidy eusocial insect is the honey bee (*Apis mellifera*). Honey bees have one fertile queen, the rest of the females being sterile workers. The males, or drones, are peculiar in only having half of the normal diploid genetic component. Therefore, a male passes on all of its genes to its offspring and as a consequence sisters share  $\frac{3}{4}$  of their genetic material with each other instead of the normal  $\frac{1}{2}$ . As a daughter to any of these sisters would only inherit  $\frac{1}{2}$  of her mother's genetic makeup it is more beneficial for a female, in terms of propagation of her genes, to forego reproduction and

become a worker, thus helping the colony so that the queen can produce more sisters (Slater, 1999).

While inflated relatedness can account for altruism in a haplodiploidy society, it is not a prerequisite. Termites (*Rhinotermitidae*) operate under a normal diploid mating system, yet live in a colony with one breeding king and queen pair and many sterile workers. How then can the genetic costs of sterility be outweighed by any benefits of being a worker? Quite simply termites could not survive without a mound to live in and that requires the help of others to build. The king and queen do not give any parental support but do produce a large supply of brothers and sisters. If it wasn't for the workers, these brothers and sisters and indeed the workers themselves would die (Manning & Dawkins, 1998b). The benefit, again, is accrued through inclusive fitness.

Eusociality in mammals is very rare, one of only two known examples being the naked mole rat (*Heterocephalus glaber*), a group living subterranean rodent in which many individuals completely forgo breeding. Like the termites and their mound, the naked mole-rats are constrained to their burrows. Being poikilotherms many workers are required to keep the burrow warm and the difficulty in gathering food requires many workers to bring back resources. Again, a pair of naked mole-rats could not survive to breed on their own and so an altruistic strategy provides the genetic benefits of inclusive fitness, increased as it is by their high degree of inbreeding (Manning & Dawkins, 1998b).

Of course, altruism need not be so extreme and cooperation, or helping behaviour, is observed in many animal societies. Belding's ground squirrels (*Spermophilus beldingi*) alarm call on sight of a predator, warning others of danger but also making themselves more conspicuous to that danger. Males

disperse in this species and do not mix with the groups of females and young. It has been found that the individuals most likely to alarm call are females with offspring and other close relatives nearby (Slater, 1994). This suggests that both direct and inclusive fitness may play a part in the maintenance of this behaviour through the saving of both offspring and kin.

Helping is common in birds and is known to occur in over 200 species (Manning & Dawkins, 1998b; Slater, 1994). For instance, in the Florida scrub jay (*Aphelocoma c. coerulescens*), the extra feeding and protection afforded by helpers increases fledgling survival from 0.56 to 1.62 young per breeding pair. Helping is preferentially directed towards related young and no difference in survival rates between helpers and non-helpers suggests that helping is not overly costly in this species (Mumme, 1992). Evidence from the Seychelles warbler (*Acrocephalus sechellensis*) suggests that benefits of helping may not just accrue through indirect fitness benefits but also through the act of helping itself. In this species the experience of nest building, incubation and clutch guarding directly increases the reproductive success of the helper when it becomes a breeder itself through having greater hatching success and a shorter time to production of the first fledgling (Komdeur, 1996). Kinship is therefore an important factor but not necessarily the only means for the maintenance of cooperative behaviour. For example, cooperation can also be observed in coalition support of white-nosed coatis (*Nasua narica*) (Gompper et al., 1997), allogrooming in impala (*Aepyceros melampus*) (Hart & Hart, 1992) and capuchin monkeys (*Cebus apella nigrinus*) (Di Bitetti, 1997) and pride defence in lions (*Panthera leo*) (Grinnell et al., 1995).

Much work has concentrated on the most extreme, complex and obvious forms of cooperation and the mechanisms maintaining them. However, to understand the evolution of such systems it is necessary to take a step back and look at the basic principals through which such systems can arise. Aggression reduction is perhaps the most basic of social behaviours and may be the first step to a more structured social organisation. When animals come together they are forced into increased competition with conspecifics for resources and this often leads to aggression. This aggression may also have a cost, however, and this cost will facilitate its mediation. In many instances the danger of physical injury resulting from conspecific aggression can be reduced by communication through displays of strength or status. Examples of such agonistic displays are as varied as roaring and parallel walking in red deer stags (*Cervus elaphus*) (Manning & Dawkins, 1998a), colour displays in male red-collared widowbirds (*Euplectes ardens*) (Pryke et al., 2001), head up displays of great tits (*Parus major*) (Wilson, 1992), and 'skraa' calls of bower birds (Borgia & Coleman, 2000).

Aggression reduction may also be facilitated through familiarity of individuals. A study on sticklebacks (*Gasterosteus aculeatus*) has shown that when competing for a resource aggression is a function of familiarity. Therefore if familiarity between individuals is allowed to build up over time, aggressiveness decreases and sharing of the resource increases (Utne-Palm & Hart, 2000). For this to operate individuals must be able to discriminate between familiar and non-familiar conspecifics and indeed individual recognition has been shown to facilitate specific aggression reduction in a range of species including turnstones (*Arenaria interpres*) (Whitfield, 1986), swordtails (*Xiphophorus nigrensis*, *X. multilineatus*) (Morris et al., 1995), sea trout (*Salmo*

*trutta*) (Hojesjo et al., 1998), stickleback (Utne-Palm & Hart, 2000), rainbow trout (*Oncorhynchus mykiss*) (Johnsson, 1997) and in the lesser white-toothed shrew (*Crocidura suaveolens*), where familiarity leads to a decrease in aggression and an increase in social behaviour (Zuri & Rado, 2000).

### 1.1.2 Theory of cooperation

As described later (Section 1.6.2), the most common form of interaction between breeding female grey seals is aggressive and this may have costs in terms of reproductive success (Anderson et al., 1979; Anderson & Harwood, 1985). If familiarity is a possible mechanism through which aggression reduction can occur, then how would this operate in the grey seal model? Little evidence has been found of local kin aggregations in grey seals suggesting that cooperation is unlikely to be sustained through the benefits of inclusive fitness (Hamilton, 1964; Pomeroy et al., 2001). Therefore the benefits of cooperation must be available to each participant to increase their own fitness. Where cooperation is in the form of aggression reduction on the part of both participants this may be the case.

It has been shown in scuirid species that an increase in social complexity of a system is associated with increased time to first reproduction, decreased litter size and increased first year survival (Blumstein & Armitage, 1998). Grey seals have a long time to recruitment and produce only one pup per year, but have high infant mortality (Hewer, 1964; Hall et al., 2001). Therefore, if conditions on the colony are able to affect infant mortality (eg. through producing bigger pups that are better able to survive outwith the colony) then an increase in social complexity such as cooperation through aggression reduction

may be of benefit. This benefit, however, may only be one of many factors affecting infant mortality. An example of cooperation with associates comes from the vampire bat (*Desmodus rotundus*), a mildly polygynous mammal with small litter size and high infant mortality. They have been shown to share blood (food) with unrelated individuals with whom they are associated. Female vampire bats display philopatry but the low survival and occasional inter-group exchange of individuals negates the possibility of kin selection, as shown by genetic heterogeneity (Wilkinson, 1985b; Wilkinson, 1985a). In the fruit bat kin selection is also unlikely to be responsible for the formation of cohesive harem groups due to the dispersal of both sexes and low survival (Storz et al., 2001).

The mechanism for cooperation without relatedness is that of reciprocity which can best be described through the Iterated Prisoners' Dilemma (IPD). The IPD describes a paradigm of repeated contact with the possibility for cooperation or defection (Axelrod & Hamilton, 1981). Within this paradigm the reward for defecting (T) is greater than the reward when both participants cooperate (R), which is greater than the reward or loss when both participants defect (P), which is greater than the reward or loss when defected against (S). Grey seals are known to aggregate around topographic resources such as pools of water (Anderson, 1975; Twiss et al. 2000, 2001). In this case T would be the benefit gained by being aggressive to an unaggressive individual and so gaining access to a pool. R would be the benefit of unaggressively sharing the pool with another. P would be the loss to an individual if both participants were aggressive and so the pool is not shared. S would be the loss to the unresponding recipient of aggression who therefore loses access to the pool. So long as the above holds and individual recognition and memory acuity allow for the discrimination of

previous encounters a Tit For Tat strategy is effective. This is when on first encounter an individual will cooperate, responding in subsequent encounters in the way that the other participant acted in the previous. Therefore, an individual that cooperates will be cooperated with and an individual that defects will be defected against. This happens so long as there is an unknown number of future encounters, otherwise the prevailing strategy is always to defect. This is the case unless cooperation directly benefits the cooperator in terms of having a player left to cooperate with in the next encounter. This Mutual Dependence IPD is most likely in antipredator cooperation where group size may be important for survival. Defection, however, will always be the best strategy in the final encounter (Lima, 1989). Mutual dependency is seen in male lions protecting their pride from invaders. If a pride is lost to a group of males then lifetime reproductive success ends for each of those males. Therefore, protection of the pride through cooperation is of considerable mutual benefit. Lions have been shown not to use a Tit For Tat strategy as they do not monitor the other pride members when reacting to invaders. They would therefore not know if they were being defected against and so rely on the need to protect the same resource for the basis of cooperation (Grinnell et al., 1995). When observing cooperation it is also important to observe time scale. If the benefit of cooperation is immediate then cooperation may be said to be through mutualism, however if benefit is accrued in the future then cooperation may be said to act through reciprocity (Mesterton-Gibbons & Dugatkin, 1997).

The assumption of cooperation on first encounter in the Tit For Tat strategy does not fit the model of cooperation through reduced aggression only with familiar individuals. Keller (1998) states that cooperation is rarely all or

nothing. Therefore in a more realistic IPD where cooperation has a variable investment a different strategy, Raise The Stakes, supersedes that of Tit For Tat. This strategy allows players to start off with a small investment, thus minimising initial cost, and increase investment with a build up of familiarity and trust. This strategy is the most likely in a real situation such as a grey seal rookery. More complex strategies have been suggested, for instance the Standing Strategy, such that what type of action a player has previously acted against affects the decision of whether to cooperate with or defect against them. It seems though, even in humans, that this type of strategy is too complicated and will not prevail (Milinski et al., 2001). It must be remembered that when observing behaviour animals do not play by a strict set of rules and behaviour is far from predictable. The behaviour of any individual may depend on individual circumstances and even individual encounters. Factors such as condition, recent experience and conscious state may all affect any individual's reaction to another. In addition, the breeding colony consists of more than two individuals and multiple players, each in different behavioural states, will introduce further complexity.

## 1.2 The grey seal, breeding and behaviour

The grey seal is of the family Phocidae, the true or earless seals, recognisable from their lack of a pinna and inability to flex the hindflippers forward. These are distinguishable in the order Carnivora (Pinnipedia) from the fur or eared seals, family Otariidae, which have a rudimentary pinna and forward flexion of the hindflippers, and the family Odobenidae, consisting as it does of only one species, the walrus, *Odobenus rosmarus*. The pinnipeds differ from the other marine mammals, orders Cetacea and Sirenia, in that they are constrained to terrestrial breeding. Whereas the cetaceans live their entire life history in the water, pinnipeds must return to a stable substrate to give birth. Grey seals are characterised in profile by a long “Roman” nose, most exaggerated in the male. They are grey in colour, aspects of their coat ranging in hue from white to black. Sexual dimorphism is apparent, males being generally larger, darker and more broad at the shoulders. Bulls are around 236cm in length and weigh from 180-295kg, whereas females are around 213cm in length and immediately post-partum are around 190kg (Anderson & Fedak, 1985; Hewer, 1964; Pomeroy et al., 1999).

### 1.2.1 The grey seal breeding colony

The mating system of pinnipeds varies widely and this is often associated with the substrate on which they breed (Riedman, 1990). Often, land breeding pinnipeds are constrained to form dense aggregations in which polygyny is evident. However, when breeding on large expanses of fast ice (attached to land) or abundant pack ice (floating) females are much more dispersed. As such male monopolisation of mates is not possible and polygyny is less pronounced or

absent. The environment in which pinnipeds breed therefore has profound implications for mating system and social structure.

The geographical range of the grey seal extends across the North Atlantic with three genetically separate populations occupying the North West Atlantic, North East Atlantic and Baltic Sea (Boskovic et al., 1996). Timing of breeding varies with location, being late autumn in the North East Atlantic, late winter in the Baltic and mid-winter in the West Atlantic (Boness & James, 1979). Across this range there is a wide variety of substrate on which the animals breed, from sand banks to rocky shores, inland grass to ice (Hewer, 1960; Anderson et al., 1975; Boness & James, 1979; Bonner, 1981; Anderson & Fedak, 1985). North Rona is an inland grassy site on which females form moderately dense aggregations.

Females start to haul out on North Rona in late September and the breeding season lasts for 2 to 3 months. Females may haul out around three days prior to parturition (Pomeroy et al., 1994), although they have been seen on the colony up to 20 days before giving birth (pers. obs.). They may subsequently move around the colony or even return to sea but will often return to their initial site to pup (Pomeroy et al., 1994; Pomeroy et al., 1999). Grey seals are gregarious animals and choice of pupping site is influenced by the presence of seals that have already taken up residence. Growth of the colony therefore happens in a clumped fashion, with distinct areas of primary colonisation increasing in numbers over time (Anderson et al., 1975). Once the pup is born, females on North Rona typically stay near the site of birth and consequently mixing of animals on the colony is limited (Redman, 2002). On other colonies,

such as the Isle of May, females often commute to the sea and mixing is more pronounced.

The grey seal is said to be a capital breeder, a female supporting herself and feeding her pup through a short lactation period with fat reserves built up prior to the breeding season. This deviation from the mammal model is most extreme in the hooded seal, *Cystophora cristata*, which has a lactation period of only 4 days, the shortest of any known mammal, in which the pup doubles in weight before weaning (Lavigne & Harwood, 2001). Female grey seals haul out, pup, lactate, copulate and wean their pups all within 21 days. The breeding season is spread across 2 months, however, so there is a turnover of breeding females, activity building to a maximum mid season and tailing off again towards the end (Anderson et al., 1975). Between 80% and 97% of returning females produce pups, but some females appear to be more successful than others. In an 11 year study of known individuals breeding at North Rona, Scotland, some 57% of females produced 74% of all pups reaching weaning (Pomeroy et al., 1999).

Immediately after parturition a female will weigh in the region of  $190\pm 23\text{kg}$ . A mass transfer efficiency of 45% and a lactation period of 18 days is responsible for the huge increase in pup weight before weaning and the dropping of female mass to  $117\pm 18\text{kg}$ , a loss of about 39%. A pup is born at around 15kg and weaned at about 40kg (Boyd & Campbell, 1971; Hall et al., 2001). At North Rona a higher female mass is often associated with earlier birth date, increased pup growth rate and survival. If maternal expenditure is overly high in any one year then this can affect maternal post partum mass the following year and so pupping success. It is then more likely for a female to skip a year of

breeding, returning two or more years later with increased condition (Pomeroy et al., 1999). At the end of lactation a female will become receptive to males, copulating around 3 times with the same or different bulls before returning to the sea (Anderson et al., 1975).

Males, where possible, operate a female defence strategy. This is in contrast to many other pinniped males which haul out before the females and defend defined territories in which they can then attempt to monopolise copulations. Grey seal males, however, try to maintain positions amongst the females themselves, attempting to monopolise copulations in an undefined and variable area (Anderson et al., 1975; Twiss et al., 1994). Rather arbitrarily, males that are able to stay on shore in the same location for two consecutive days are said to attain “tenureship”, those which don’t being “transient” as defined by Boness and James (1979). Transients are often more mobile within the colony. Other males may not be able to enter the colony at all, staying at the periphery of the rookery or in the surrounding waters.

Tenured males are observed to acquire the most copulations, mating success increasing with duration of residence, area covered and density of females (Twiss, 1991; Twiss et al., 1994; 1998; 2003). Duration of stay of males at the rookery is highly variable ranging from a few minutes or hours up to almost two months. Median duration of stay is 2 days, males which stay longer generally being of higher dominance (Anderson et al., 1975, Twiss, 1991; Twiss et al., 1998). Males are subject to dominance hierarchies, although these are not strictly linear as reversal can occur. Thus, in some circumstances even a highly dominant male can be ousted by one of a seemingly lower rank (Anderson & Harwood, 1985; Twiss et al., 1998). When active in the breeding colony males

do not return to the sea to feed, relying instead on their blubber reserves to sustain them. A male with a lot of stored resources will therefore be able to stay active within the colony longer than one with less stored resources. The upper limit of stay for males has been estimated to be 47 days. However, as some animals can stay for up to 57 days this suggests a mechanism of decreasing energy expenditure for longer residency (Anderson & Fedak, 1985, Twiss, 1991).

### 1.2.2 Site choice and topography

Fine scale site choice on Scottish colonies seems to be predominantly based on access to water, be this the sea or inland pools (Anderson et al., 1975; Twiss et al., 2001). Access to water may be beneficial for thermoregulation and in contrast to Scottish colonies, grey seals breeding on Sable Island, Nova Scotia, where the temperature is generally lower, do not typically access water whilst breeding (Boness et al., 1979; Twiss, 2002). The importance of water has been evident through observation of an atypically dry period on the usually wet rookery at North Rona. During this time female movements increased and pup attendance decreased (Redman et al., 2001). Evidence from an expanding colony has shown that a site which was topographically less costly, i.e. one from which it was easier to access resources, was associated with older, more dominant females, increased time resting and in mother-pup interactions. At a topographically more costly site, however, there was more female locomotion, more sexual aggression and greater mother-pup separation (Twiss et al., 2000; Pomeroy et al., 2000a). Topography therefore plays a major role in site choice and indeed the most appropriate sites for breeding are those which are colonised first (Pomeroy et al., 2000a; Pomeroy et al., 2001). Just as the substrate on

which animals breed has implications for sociality, then, the fine scale topography of sites may also effect patterns of aggregation and so social behaviour .

### 1.2.3 Philopatry and site fidelity

Both sexes of grey seals have been shown to display some degree of philopatry, returning to their natal site to breed (Pomeroy et al., 2000b). Evidence of philopatry is difficult to establish due to the long time from birth to recruitment and high mortality rates adversely affecting sample sizes, however, genetic evidence describing differentiation between two commutable rookeries in Scotland suggests that there is little mixing between colonies (Allen et al., 1995). Grey seals also display fine scale site fidelity, returning to pup in the same place in successive years. This is not affected by pupping success history, in contrast to elephant seals which are more likely to change site after an unsuccessful year (Reiter et al., 1981). Female grey seals display strong site fidelity, returning to a median of 33m from previous pupping sites on North Rona, and 14m on the Isle of May, Scotland (Pomeroy et al., 1994; Pomeroy et al., 2000b, Redman, 2002).

Philopatry and site fidelity are by no means an artefact of colony isolation. Grey seals are able to travel long distances in excess of that which separates many breeding colonies (McConnell et al., 1999). Although philopatry and site fidelity are definitely displayed by these animals they are by no means exclusive strategies and there are many examples of seals moving from one site to another (see: Pomeroy, 2000b). Grey seals also display fine scale temporal fidelity to previous breeding activity, varying in date of pupping by only a few days between years (Pomeroy et al., 1999).

Such evidence of high site and temporal fidelity between years and limited mixing within years provides the scope for repeated and prolonged associations to occur between females, suggesting the possibility for relationships to form (Hinde, 1981). In turn, this possibility, whether actively or passively promoted, sets the scene in which sociality may develop (Michod, 1999).

#### 1.2.4 Conception, parturition and survival

Follicular growth starts at parturition, with oestrus occurring at the end of lactation (Boyd, 1983). After fertilisation, delayed implantation acts to suspend development for around 135 days. The blubber which was lost through lactation is not replaced until just before implantation and for animals pupping in November this takes place around the same time as the annual moult, in early spring (Boyd, 1984). Both sea surface temperature and size of previous years colony have been suggested to affect timing of breeding, perhaps by influencing the timing of delayed implantation, although there is little evidence to support this (Coulson, 1981). After implantation foetal growth rate is steady and at parturition the sex ratio is 1:1 (Boyd, 1984; Hewer, 1964).

Although uncommon on North Rona (pers. obs.), there is considerable evidence of allo-suckling and non-filial nursing by grey seal females. However, genetic data suggests that this is most likely explained by inexperience or ineptitude rather than kin selection (Perry et al., 1998). Mass of yearlings has been reported to be less than that of weaners which suggests that pups use up the blubber reserves supplied to them by their mother before learning to feed (Hall, 2001). However, a laboratory case study has shown that weaners have the ability

to catch prey only 8 days after weaning (Kastelein et al., 1995). It should be noted that the body composition will change dramatically between weaning and the end of the first year as a seal uses up blubber and starts to lay down lean body mass.

Time to first breeding has been recorded as between 4 to 10 years for females and males are typically not able to gain position in a colony until about 7 to 10 years (Hewer, 1964; Pomeroy et al., 2000b; Pomeroy et al., 1999, Twiss, 1991). Age can be determined by examination of the cement layers of the canine teeth, and individuals up to 36 years of age have been recorded in the breeding colony (Hewer, 1964; Pomeroy et al., 1999). Males, however, are typically only reproductive on the colony for a few years (Twiss, 1991). There is therefore the possibility for overlap of generations, offspring of an individual being recruited into the breeding population before the parent has left.

Many animals suffer high mortality rates in the juvenile stages and grey seals are no exception. A study on North Rona in 1975 indicated that 35% of pups do not survive to leave the island. However, pup mortality rates vary hugely with location even on a sub-colony scale, ranging in this instance from 18% to 61% in different regions of the island (Summers et al., 1975). In 1979 a study on Ramsey, Dyfed, and Auskerry, Orkney, indicated pup mortality rates of 35% and 14% respectively. Ramsey is a more exposed site and the extra mortality was accounted for by animals being lost to the sea (Anderson et al., 1979). This reinforces the idea that location and topography of breeding site are very important factors in grey seal life history, even on a fine scale.

The majority of pup deaths are due to a disturbance of the mother-pup bond, poor nutrition predisposing pups to further problems. Also, the unhealed

umbilicus is a very susceptible area to a wide variety of infections (Anderson et al., 1979; Baker et al., 1998). Pup mortality on North Rona is greater in areas of reduced habitat quality suggesting that either habitat quality itself or characteristics of the animals within different habitats affects pup survival (Twiss, 2003). Density of females was not related to pup mortality.

Pups that survive to weaning should weigh approximately 40kg, males being slightly larger than females. First year survival rates have been estimated to be in the region of 60% and a study of dead, stranded animals has reported the main causes of weaned pup mortality to be starvation and pneumonia (Baker et al., 1998; Hewer, 1964). First year survival is dependant on weaning condition and sex, females from the Isle of May, Scotland having a survival rate of 0.6 compared with the value for males of 0.2 (Hall et al., 2001).

Causes of mortality in juveniles have been accredited mainly to drowning in fishing gear and starvation, while in adults they have been accredited to respiratory diseases. These conditions are a far from exhaustive list of the fatal and non-fatal conditions suffered by seals, though, small sample sizes and a wide variety of conditions providing inconclusive evidence as to the predominant causes of death (Baker et al., 1998).

#### 1.2.5 Mating system and genetics

Most mammals are said to be polygynous and indeed that is what appears to be the case in grey seals through behavioural observations (Le Bouf, 1991; Davies, 1991). A few top males are seen to be the most behaviourally dominant, stay longest and mate with the most females (Twiss et al., 1994; Anderson et al., 1975). Genetic studies, however, have shown that the mating system may in fact

be much less clear cut. In an highly polygynous system paternity of offspring is highly skewed, a few highly successful males having elevated fitness, siring most offspring. Dominant grey seal males sire the most offspring but do not have such a monopoly as the behavioural data might suggest. Over a ten year study at North Rona and the Isle of May, Scotland, only 36% and 23% of paternities respectively could be assigned from the males sampled in the rookery, i.e. those which could have been assigned a dominant status (Worthington Wilmer et al., 1999). The rest of the paternities must therefore be from unsampled males, be they unsampled tenured males, transients, males on the periphery of the rookery, males in the water or even from another site entirely. Possibility of paternity, of course, depends on where the respective mother was in the year of conception. In a sub-sample of the North Rona data, when the paternity could be assigned, 89% of the time this was from a male who had been observed near the mother (Amos et al., 1993). Indeed, on both islands 5 individual males did enjoy the most reproductive success, however, the majority of males do appear to succeed in fathering a pup (Worthington Wilmer et al., 1999; Worthington Wilmer et al., 2000). This evidence suggests that having a behaviourally dominant position does accrue a fitness benefit but less than would be expected from behavioural observations alone. The grey seal could therefore be said to operate under moderate polygyny, a scenario repeated in other species, once thought to be more highly polygynous, for which there is new genetic data, for instance prairie dogs (Travis et al., 1996) and coatis (Gompper et al., 1997).

A limitation of recent grey seal genetics, however, is that it has been based on large data sets without reference to the individual and caution must therefore be taken in its interpretation. Without direct reference to the individual

one does not know where a female was in the previous year when conceiving, only in the sample year when giving birth. As some females skip breeding years and others move to non-breeding haulouts, where they could be mated separate from the breeding colony, it may be expected that when included in the analysis, these individuals would dilute the apparent dominance of the resident males (Pomeroy et al., 1994). Perhaps, then, a more rigorous approach is needed linking observational data from one year with genetic data from the year after. Then, paternities from resident males could be assigned to only those pups whose mothers were available to them. A more complete sampling of males other than residents would be useful for determining the distribution of paternities between the different classes of males. This 'bottom-up' approach of elucidating life history strategy from individual data may prove more exact than the 'top-down' approach of estimating individual behaviour through general trends.

There are two main arguments as to what reduces the dominants' monopoly, male aggression and female choice. On Sable Island, Nova Scotia, 43% of paternities were assigned to non-attending males. Behavioural data showed that most of these extra consort copulations took place where female density was highest suggesting that this gave extra consort males more opportunity to forcibly poach females (Ambs et al., 1999). However, behavioural observations tend to show that female aggression is the determining factor in most successful copulation attempts by males and this would suggest female choice (Anderson et al., 1975). Females display more aggression towards males than they do to females and this could perhaps function in assessing male quality (Boness et al., 1982; Anderson et al., 1975; Zuri & Rado, 2000). In addition, when approached by a male, female aggression often arouses the

attentions of another male, making an interruption of mating more likely and so inciting male competition (Boness et al., 1982). This would be an indirect mechanism for female choice. Female choice is also supported by the finding of mate fidelity through a higher proportion of full siblings than would be expected by either chance or even site fidelity at North Rona (Amos et al., 1995). Also, while full siblings are present, maternal half siblings may be more heterogeneous than expected by chance, suggesting female choice for diverse partners (Amos et al., 2001a; Amos et al., 2001b; Worthington Wilmer et al., 2000). As many paternities can not be assigned to the behaviourally dominant males and there is evidence for the operation of female choice, there is also the possibility of females using males not as reproductive partners but as social partners. That is, perhaps tenureship by a dominant male is useful to the female in that it provides a secure place to pup even if she doesn't mate with him.

As outlined above, individuals often return to the site of their birth and often return in successive years to previous pupping sites. In addition to this the time to recruitment is less than that of the reproductive lifespan of some individuals and the presence of full siblings demonstrates the presence of mate fidelity. Therefore, it is possible that young seals may be recruited into the colony, assuming positions close to those of close relatives. This suggests the possibility of local kin aggregations occurring within a colony and it is in situations such as this that cooperative, kin selective behaviours can arise (Hamilton, 1964; Taylor & Irwin, 2000).

The structure of relatedness between individuals within grey seal colonies has been studied on the rookery at North Rona. Here it was found that pairs of individuals were no more related to each other when the distance separating them

was small than when it was large (Pomeroy et al., 2001). This analysis was carried out at a 20m scale and suggests that related individuals do not preferentially aggregate together at this scale. Perhaps a limitation of this is that average values for each 20m bracket represent the colony as a whole, whereas kin groups may only be represented by a few individuals. The lack of evidence for kin aggregation within close proximity may therefore be a result of dilution by non-kin also within that proximity. However, it has been found that there are specific areas within the colony in which the occupants are more related to the colony as a whole than the average. This suggests that individuals within these areas are of high fitness, being the primary source of genes for the colony. The hotspots which these females occupy are also associated with favourable topography, being low-lying and at optimal distance to the sea. These are also the areas which are colonised first within each season and by the most successful females. In addition to this, pups born within these areas benefit from increased growth rate, even when maternal mass is accounted for, indicating the ability for greater provision for young within these areas. However, understanding whether these factors pertain to quality of the areas themselves or to the individuals who inhabit them is necessarily difficult.

#### 1.2.6 Aggression

Aggregation of females on the breeding colony appears to be primarily governed by access to topographical resources (Twiss, 2000; 2001), but although gregarious individuals are antagonised by close proximity to others. This leads to a show of aggression, if not physical attack (Hewer, 1960; pers. obs.). Female aggression is dependant upon a number of factors. Pregnant females seem more

tolerant of each other than do females with pups, often forming more dense groups. When a female has pupped, however, and the intruder in question is female, then the likelihood of an aggressive response increases with both proximity and whether or not her pup is between herself and the intruder. This is most pronounced with a young pup, aggression decreasing towards the end of lactation (Boness et al., 1982, Redman, 2002). Female aggression to males is independent of pup position and tends to be incited over greater distances than that to females. Occurrence of aggression to male approaches does not, in general, tend to decrease during lactation, unless the male is successful in mounting (Boness et al., 1982). Grey seals of both sexes spend between 66% and 80% of their time ashore resting and this has been hypothesised to be for conservation of energy while fasting. When active, however, the most common forms of behaviour are either alert or agonistic (Anderson & Harwood, 1985). Aggression is therefore of importance to grey seal individuals, much active time and energy spent on personal vigilance. In such a system the ability to reduce aggressive behaviour may be beneficial, so long as aggression really is costly and the time and energy benefits accrued from reducing it could make a difference to lifetime reproductive success.

Aggression reduction is evident in sexual conflict between grey seals, familiarity of a male decreasing female aggressive response (Boness et al., 1982; Twiss et al., 1994). It has also been suggested that males may reduce aggression with neighbouring males after initial conflicts (Twiss et al., 1994). If such conflict reduction is present between female grey seals it would be beneficial to familiar individuals sharing limited topographical resources. Familiarity may build up within a season as movement of females is limited and across seasons if

site fidelity brings individuals into repeated contact (Anderson & Harwood, 1985; Pomeroy et al., 1994; Pomeroy et al., 2000b). In this case we may expect to find groups of previously associated mothers in areas where levels of aggression are lower than the average. In turn these areas may be associated with the previously found “hot-spots” of most favourable topography and increased pup growth (Pomeroy et al., 2001).

### 1.3 Individual Recognition

If grey seals are able to act in response to previous encounters then they must also be able to discriminate between individuals. The exact mechanism by which this may be done is unknown, however there are various possibilities. The major histocompatibility complex (MHC) is a part of the genome associated with immune response. Diversity of the MHC is maintained in populations and it has been suggested that MHC is advertised through chemical olfactory cues allowing for kin recognition and so mate choice to avoid inbreeding (Tregenza & Wedell, 2000). Some work on Soay sheep (*Ovis aries*), however, suggests that maintenance of MHC diversity is through parasite pressures and is not associated with mating system (Paterson & Pemberton, 1997; Paterson et al., 1998). Major Urinary Proteins (MUPs) have also been suggested to advertise identity and may even be diverse enough for individual discrimination (Hurst et al., 2001). Grey seals do appear to sniff each other (pers. obs.) and this sense may play a particular role in pup identification (Burton, 1975). Grey seal males in particular have a very distinctive odour (pers. obs.) and the olfactory sense is highly refined in the carnivores (Macdonald, 2001). Many carnivores use scat marking to display occupancy of territory and perhaps the faecal and urinary matter that accumulates around a seal's position can relay identity information. In addition, female seals can sometimes be seen clawing at the grass. No function is known for this behaviour but perhaps it is involved somehow in the laying down (or removal?) of scent.

Individual vocal recognition is observed in many animals, especially birds eg. (Lampe & Slagsvold, 1998; Chaiken, 1992). Emperor penguins (*Aptenodytes forsteri*) use a remarkable system where two syringeal bodies

operate simultaneously to produce an individual beat which can propagate well through the mass of bodies in a colony (Aubin et al., 2000). Bottlenose dolphins (*Tursiops truncatus*) also have distinctive individual calls, thought to be used for individual recognition (Sayigh et al., 1998). Long-term vocal recognition is evident in the northern fur seal (*Callorhinus ursinus*), animals responding to their mothers' calls, recorded when they were pups, after 4 years absence (Insley, 2000). In some of these examples it is unclear whether animals are able to recognise a particular individual or group of individuals from many or whether they are capable of recognising many specific individuals distinctly. Although pup calls are individually distinctive in the grey seal, mothers were not shown to be able to discriminate between own and non-filial pup calls in playback experiments (McCulloch et al., 1999).

Visual recognition has been demonstrated less often than the other senses. However, chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*) have both been shown to be capable of discriminating individual faces (Parr et al., 2000). Pigeons (*Columba livia*) are also able to discriminate conspecific faces, lesion experiments pointing to the role of the ecostriatum in this process (Watanabe, 1992). Goat kids have been shown to use visual cues in recognition of their own mother and the non-vocal turnstone is able to recognise individuals through plumage variability (Whitfield, 1986; Ruiz-Miranda, 1992). No evidence exists for visual identification in the grey seal, however their individually distinct pelage markings certainly lend themselves to be used in such a way. Indeed, that is how individuals were identified in this study. The visual system of pinnipeds is adapted mainly for good vision in low light levels under water. They are certainly able to see on land although may be hindered by

myopia and astigmatism due to the large cornea and lens needed for aquatic vision (Lavigne et al., 2001). It would be very interesting to learn more of the visual capabilities of grey seals and whether visual recognition is possible in this species. Because pelage pattern is primarily gene controlled (see below), this may provide a basis for not only individual but also kin recognition.

### 1.3.1 Pelage patterns

The dark markings on mammalian coats are due to melanin producing melanocytes in the epidermis. The pattern of melanin production is gene controlled, set up by a reaction-diffusion model of activators and inhibitors in the embryo. All other parameters being equal size and shape of the body determines the form of pattern produced. As size increases the pattern produced by the reaction-diffusion model changes from uniform through simple to complex and then to so complex as to be almost uniform again. It is possible that this describes the differences between the sexes of grey seals, mature males being larger and more uniform of pattern than females. However, many other parameters such as humidity, diet, hormone levels and metabolic rate may also affect pattern production, producing randomness and so variety. Temperature is known to affect pattern production in Siamese cats, cooler areas at the extremities during the time of pattern formation producing more melanin and so being darker. Genetic factors such as the timing of genetic switches or the threshold level for melanocyte activity may also act to alter the end product of pattern formation (Murray, 1981; Murray, 1988). Perhaps one pattern formation is responsible for the simple dorso-ventral shading in the grey seal and another for the more complex spot patterning.

Genetic and environmental control of patterning is highlighted in cheetahs. Cheetah siblings are more similar in tail pattern to each other and their mother than would be expected by chance. However, siblings are more similar to each other than they are to their mother. This suggests both heritable genetic control and environmental influence in the womb (Caro & Durant, 1991). Primary genetic control of markings has been illustrated in the decreasing numbers of Iberian lynx where genetic drift has acted to eradicate pelage types of low frequency (Beltran & Delibes, 1993).

The function of a pattern must, of course, be examined in the context of the habitat in which it is found. In general it seems that spots function as camouflage, tail patterns act in communication and eye spots improve vision (Ortolani, 1999). In the grey seal, as with other phocids, the function of spotted pattern may therefore have evolved as an aggressive camouflage for concealment from prey. If this is the case then it is possible that visual recognition has become available to phocids as a by product of their individual camouflage patterns. Otariids, of course, which are thought to feed in much the same way, are largely uniform in pattern (Ortolani, 1999).

### 1.3.2 Photo Identification

There are various ways in which animals can be tracked for repeated sampling in the wild. Previous studies on grey seals have used brands, tags and paint/bleach to artificially mark animals for individual identification (Boyd & Campbell, 1971; Perry et al., 1998; Pomeroy et al., 1994). This allows for behavioural and physiological data to be gathered over extended time periods without the risk of losing individuals in the throng of the rookery. Brands are

life-long markings and tags have reasonable retention rates and so individuals marked in this way can often be tracked not just within a season but between years too (Harwood et al., 1974; Pomeroy et al., 1994). While useful, however, these techniques do have their drawbacks. Branding, although highly visible, requires immobilisation, handling and permanent deformation of the study animal and so requires ethical considerations. Tagging also requires disturbance of the study animal for attachment and as tags can be very difficult to read, close up observation or physical contact is often necessary for subsequent identification. With both methods disturbance of the study animals and their surroundings are therefore necessary.

Grey seals are already individually identifiable by their unique natural markings and this can be used to the researcher's advantage, in some circumstances making the need for artificial tags obsolete. Pelage patterns are a reliable source of identification for female grey seals as they are stable throughout an animal's life (Vincent et al., 1999). Individual recognition by natural markings has been used extensively in studies on many other animals, for instance leopards (*Panthera pardus kotiya*) (Miththapala et al., 1989), cheetahs (*Acinonyx jubatus*) (Caro & Durant, 1991) and lions (*Panthera leo*) (Pennycuik & Rudnai, 1970). Photographic identification is a hugely useful tool allowing post hoc identification of a much larger sample size than would be possible if identification had to take place in situ (Hammond et al., 1990b; Kelly, 2001). It is also possible to record any individual, whether or not they have been captured before, without the need for disturbance. This is because animals can be recorded from a distance, without any physical contact. The draw back of this, however, is that orientation and position of the study individuals and adverse

weather conditions can result in unusable images. Poor quality photographs account for the most errors in photo ID surveys. To combat this an image scoring system is often used and poor quality images discarded (Stevick et al., 2001). Two types of error are possible, false positive identifications and false negative identifications (Hammond et al., 1990a). It has been suggested that risk aversion may reduce false positive errors but that worker inexperience and fatigue may increase error rate (Katona & Beard, 1990; Stevick et al., 2001). The most common cause of a false negative error must be the non-matching of left and right side photographs. In the field it is often very difficult to get good shots of both sides of an animal in the same sitting and this means two photographs from different sides of the same animal will be recorded as being from two different animals. Humans are capable of quite remarkable feats of identification, however, one example being a fieldworker who was able to identify from memory 29/30 good images and 23/30 poor images from a pool of 100 photographs of a flock of 850 swans taken 14 days previously (Bateson, 1977).

One way to decrease error rate is to increase the amount of information on which to base a judgement. For instance, in a study of lions, identified by vibrassa spot patterns, it was calculated that 13 bits of discrete information were necessary to identify individuals at the 1% level from a population of 1000 (Pennycuik & Rudnai, 1970). Clearly then it is necessary to score as much of the body as possible to make identification as accurate as possible.

An aid to visual identification is available in the form of computer-aided matching (Hiby & Lovell, 1990; Kelly, 2001; Mizroch et al., 1990; Whitehead, 1990). This is an automated process which matches digitised data within a

catalogue. The matches that the computer generates can then be confirmed by eye. In the case of the grey seal a grid is identified on the neck of each photographed individual. This digitised grid is given a numerical description based on greyscale values, which can then be referred to that from other photographs (Hiby & Lovell, 1990). This can be done on a desktop computer, each pair-wise comparison taking less than 2 seconds. Although very useful this system only uses one part of the whole-body pelage and also suffers the necessity for good orientation and lighting of the original photograph. Computer aided matching also requires better quality photographs than are needed to match by eye (pers. obs.). The recent development of digital camera technology has transformed the process of photo identification allowing very large sample sizes to be collected and stored cheaply and with instantaneous accessibility. As such the role of computer aided matching is likely to become all the more important in future.

#### 1.4 Overview

Female grey seals form large aggregations in the breeding season, where they undergo an intensive period of lactation before weaning their pup, mating and returning to the sea (Hewer, 1964, Anderson et al. 1975, Pomeroy et al., 1994). Within the Scottish breeding colonies animals aggregate around topographical resources (Anderson et al., 1975, Twiss et al., 2000; 2001) and there is a high premium for individual space. The most common type of interaction within the colony is agonistic (Boness et al., 1982). Aggression, however, may also have associated costs, such as the risk of injury, energy expenditure and reduced maternal care. Clearly then, the ability to reduce aggression may be beneficial. Site and temporal fidelity of females between seasons and limited mixing within seasons suggests the possibility that both repeated and prolonged associations may occur (Pomeroy et al., 1994; Pomeroy et al., 2000b; Redman, 2002). These associations are the prerequisite for relationships and further sociality to develop (Hinde, 1981; Michod, 1999). Familiarity between associated individuals is often associated with a reduction in aggression (for example: Utne-Palm & Hart, 2000; Whitfield, 1986; Zuri & Rado, 2000). If individual recognition allows familiarity to develop between female grey seals then this may provide the opportunity for a reduction of aggression and increase in maternal performance. Familiar individuals would therefore be expected to maintain association by maintaining proximity and thus providing an environment of increased social stability within which to raise a pup. It is therefore hypothesised that social stability on the colony will be associated with reduced aggression and increased maternal performance. In addition, as prime habitat has been associated with elevated maternal attendance

and performance (Pomeroy et al. 2001; Twiss, 2000; 2003), areas of elevated social stability may also be expected in areas of high topographic quality. Evidence of such would provide clues as to the mechanisms by which a basic social structure can be promoted and persist in an otherwise apparently loosely organised aggregation.

#### 1.4.1 Thesis structure

The general methodology of data collection for this thesis is described in Chapter 2. Chapter 3 is concerned with the description of fine-scale behaviour within the colony. In doing so it is sought to not only describe the behaviours displayed but to better understand the context of social interactions and so how best to measure them. Specifically, the spatial scale over which interactions take place will define the spatial scale over which associations should be measured. In Chapter 4 a method is devised with which to describe sociality within the breeding colony both within and between breeding seasons. This definition must be both practical and relevant to the type and extent of associations that female grey seals display. Chapter 5 is concerned with the description of within year sociality, using the measure and scale devised above, within two breeding seasons on North Rona. The performance of the methodology is assessed. Variation in sociality may occur for a variety of reasons and so evidence of active social behaviour is sought by testing observed data against null model simulations of non-social behaviour. Relationships between sociality, the natural environment, aggressive behaviour and ultimately maternal success are investigated. Chapter 6 is concerned with a similar description and test of sociality between the two consecutive breeding seasons in this study, thus

investigating the possibility of long term social processes. The results and their implications are discussed within the context of the literature in detail throughout the thesis and more broadly in Chapter 7.

# **Chapter 2**

## **General Methods**

## 2.1 Study site

North Rona (59°07'N, 05°49'W) is a remote and uninhabited North Atlantic island that lies 75.5km NNW off Cape Wrath, Scotland. The island consists of approximately 1.2km<sup>2</sup> of grassland surrounded by cliffs and rocky shores. The highest point of 108m lies on a central hill that drops quickly to a low lying peninsula and cliffs in the north and slopes to sea cliffs in the south. North Rona has been a major breeding site for grey seals since the late 19th century (Boyd & R.M., 1962) and as such is designated as a Special Area of Conservation by the European Commission and the Joint Nature Conservation Committee (JNCC.gov.uk).

Extensive studies of the North Rona seal colony have been undertaken since the 1960s (Boyd et al., 1962). The main breeding aggregation of grey seals is located on Fianuis, the low lying northern peninsula. Animals haul out by way of gullies on the eastern coast and move up to 300m inland to breed. The Fianuis peninsula was divided into three regions by Pomeroy et al. (1994) (see Figure 2.1.1, reproduced from Pomeroy et al. (1994)). The Study Area (SA) in particular has been the focus of detailed observations (Pomeroy et al., 2001; Pomeroy et al., 2005; Twiss, 1991; Twiss et al., 1994; Twiss et al., 2002; Twiss et al., 2003). The study area of primary attention in this thesis was contained within the SA of Pomeroy et al. (1994). Figure 2.1.2 shows the boundaries of the study area in 2002 and 2003. This area was chosen to be of a size within which all animals could feasibly be identified, to incorporate a variety of terrain, pool availability and access to the sea and to reduce edge effects by encompassing primary aggregations of animals. The area increased in size from approximately

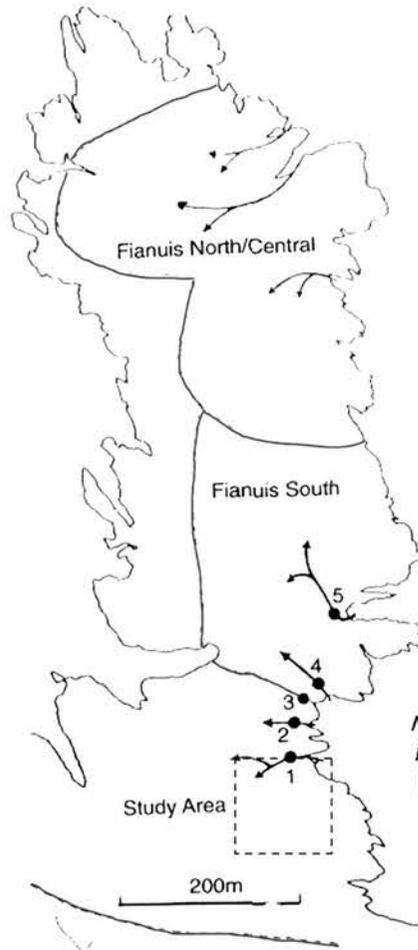


Figure 2.1.1. Reproduced from Pomeroy et al. (1994) Figure 1 pp 431. Sub regions of North Rona grey seal breeding colony. Fianuis North / Central (FN / FC), Fianuis South (FS) and Study Area (SA) are delineated in red. The approximate extent of the study area in 2002 and 2003 is delineated in blue. Arrows indicate access gullies from the sea. Gullies 1 to 5 serve FS and SA.

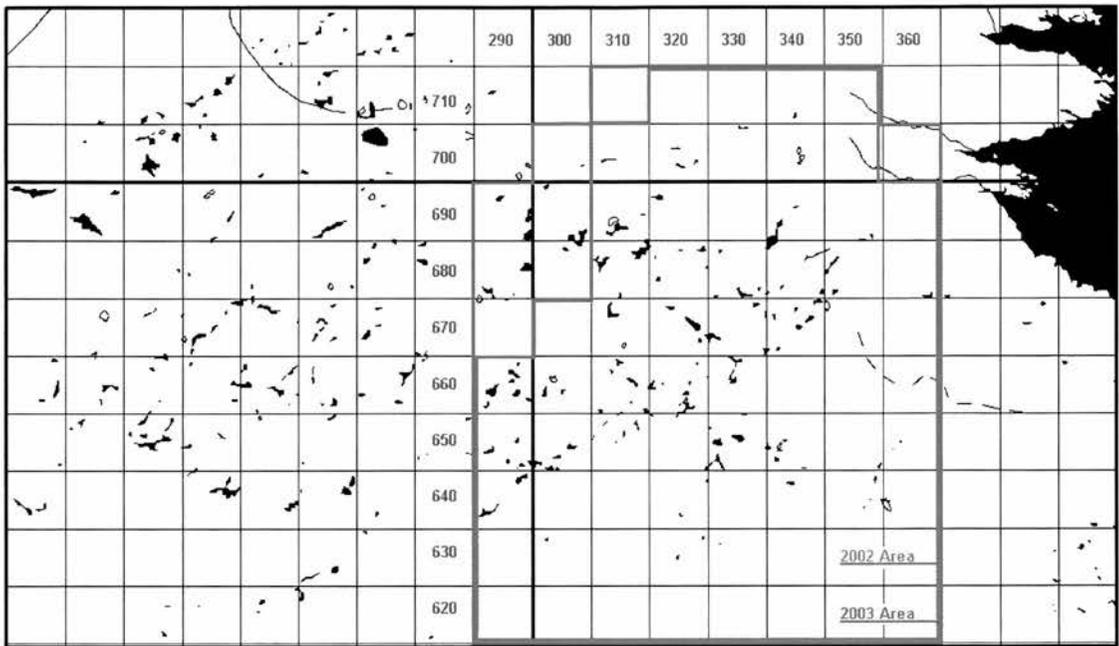


Figure 2.1.2

Study areas in 2002 (green) and 2003 (red)

Black objects denote physical features such as rocks, pools and sea.

X axis represents OSGB eastings (prefix 181\*\*\*).

Y axis represents OSGB northings(prefix 1032\*\*\*).

Map units are in metres.

6800m<sup>2</sup> in 2002 to 7600m<sup>2</sup> in 2003. The study area is overlooked by Leathad Fianuis, a high ridge, from which observations were made.

## 2.2 Equipment

Remote observation and image capture of animals in the study area was carried out from Leathad Fianuis, at a distance of approximately 150m and 50m elevation. Image capture was carried out using a Canon EOS D30 digital SLR camera and Celestron G-8 2032mm focal length F/10 telescope, connected directly using a T-mount. This allowed full body images of animals within the study area to be taken. Photographic quality has the potential to provide a significant source of error to photographic identification studies (Stevick et al., 2001). Much effort was therefore put into acquiring consistently good images. The most detrimental process to image quality in this study came from weather conditions, particularly buffeting from wind. Movement of photographic equipment results in the blurring of images and this is most pronounced when using extreme focal lengths. To this end a hide was constructed to shelter the equipment from the elements while maintaining an ample field of view. In addition, photographs were always taken in pairs, one at metered exposure and one at -1EV exposure to increase shutter speed. Images were written to an IBM microdrive and transferred to CD for storage. Short range image capture was also carried out within the colony. A Canon MV30 digital video camera was used to record full body and close up video images of animals. Digital still images were extracted using Pinnacle Systems Studio DV Plus hardware and software (pinnaclesys.com). Additional short range images were captured using a Minolta Dynax 7000 SLR camera and 30-70mm lens on Ilford XP2 400 ISO monochrome film. These images were digitised using an HP PhotoSmart S20 film scanner. Images were edited where necessary using Adobe Photoshop 5LE (adobe.com).

## 2.3 Procedures

### 2.3.1 Photo identification and mapping

Throughout the 2002 and 2003 breeding seasons a series of photographic surveys were carried out in which every animal within the study area was 'captured'. The survey schedule was kept as regular as possible, although limited by weather conditions and other fieldwork constraints (Table 2.3.1.1). Each survey consisted of field identification, using sketches and the catalogue described below. This was followed by photography and mapping at 1300 hours. An instantaneous scan method was used to capture each individual. On sampling each individual was photographed and its position marked with metre accuracy on a georectified map (Twiss et al., 2000; Twiss et al., 2001). This map provided a spatially accurate and detailed fine-scale representation of the study area allowing accurate recordings of female locations. Where possible, the presence of a pup and its stage was recorded. Pup stages range from 1 (newborn) to 5 (weaned) (Boyd et al., 1962) and are useful in determining a female's stage of lactation. Post-hoc analysis of photos allowed for subsequent identification of those animals not identified in the field. Identification data are shown in Table 2.3.1.1. The final product of this was a set of maps containing the locations and identities of each animal within the study area throughout the 2002 and 2003 breeding seasons (for example see Figure 2.3.1.1).

### 2.3.2 Animal catalogue

A catalogue of images was created as a reference against which to identify animals. The process of sketching animals was deemed the best way to commit pelage patterns to memory and provided the best way of identifying

2002 Season

Date	Total	FieldID	LabID	UnID	PropID	Time Interval
01-Oct	15	10	5	0	1.00	-
02-Oct	20	8	7	5	0.75	1
04-Oct	36	13	17	6	0.83	2
06-Oct	27	16	7	4	0.85	2
07-Oct	35	19	6	10	0.71	1
09-Oct	36	16	13	7	0.81	2
10-Oct	46	24	9	13	0.72	1
12-Oct	45	25	14	6	0.87	2
13-Oct	54	22	24	8	0.85	1
15-Oct	54	24	14	16	0.70	2
19-Oct	49	19	19	11	0.78	4
20-Oct	48	20	21	7	0.85	1
21-Oct	52	23	20	9	0.83	1
24-Oct	46	22	16	8	0.83	3
26-Oct	45	27	14	4	0.91	2
28-Oct	37	21	10	6	0.84	2
30-Oct	22	13	8	1	0.95	2
31-Oct	17	12	3	2	0.88	1
01-Nov	17	15	1	1	0.94	1
03-Nov	15	11	4	0	1.00	2
04-Nov	12	9	3	0	1.00	1
05-Nov	12	8	3	1	0.92	1
<b>Total:</b>	<b>740</b>	<b>377</b>	<b>238</b>	<b>125</b>	<b>0.83</b>	

Excluded dates in 2002 season

30-Sep	16	8	3	5	0.69	innacurate mapping
05-Oct	32	16	3	13	0.59	poor photo quality
<b>Total:</b>	<b>48</b>	<b>24</b>	<b>6</b>	<b>18</b>	<b>0.63</b>	

2003 Season

Date	Total	Field ID	Lab ID	Un-ID	Prop-ID	Time Interval
29-Sep	29	11	17	1	0.97	-
30-Sep	38	13	19	6	0.84	1
01-Oct	45	19	23	3	0.93	1
02-Oct	47	26	17	4	0.91	1
05-Oct	60	23	31	6	0.90	3
10-Oct	55	24	26	5	0.91	5
11-Oct	54	32	18	4	0.93	1
12-Oct	52	25	24	3	0.94	1
14-Oct	60	33	23	4	0.93	2
16-Oct	55	25	27	3	0.95	2
18-Oct	52	24	26	2	0.96	2
19-Oct	54	34	17	3	0.94	1
21-Oct	49	34	10	5	0.90	2
23-Oct	45	27	15	3	0.93	2
25-Oct	30	22	8	0	1.00	2
27-Oct	23	19	2	2	0.91	2
29-Oct	19	18	0	1	0.95	2
30-Oct	16	15	1	0	1.00	1
02-Nov	11	10	1	0	1.00	3
03-Nov	10	10	0	0	1.00	1
04-Nov	7	7	0	0	1.00	1
<b>Total:</b>	<b>811</b>	<b>451</b>	<b>305</b>	<b>55</b>	<b>0.93</b>	

Table 2.3.1.1 Survey schedule and identification data

Total: total number of animals in study area

Field ID: number of animals identified in field

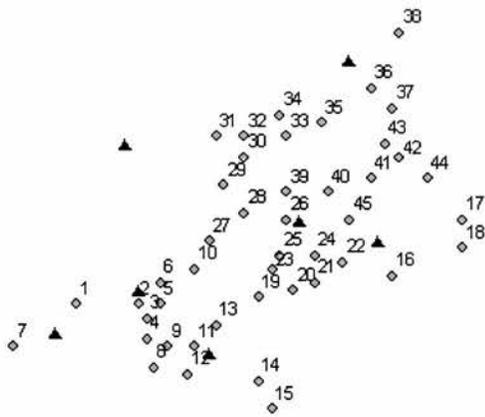
Lab ID: number of animals identified in lab

Un-ID: number of animals for which an identification was unavailable

Prop-ID: proportion of animals identified

Time Interval: number of days between surveys

Survey 10



Survey 11



Figure 2.3.1.1

Data maps and photographs of the study area on two dates in 2002

Coloured circles denote location of animal. Number denotes survey animal number. Black triangles denote physical landmarks. Note that photos are for illustration only and include females, pups and males. Photographs and map locations were recorded at different times and so discrepancies will be apparent between the two.

animals from day to day, within a season (for example see Figure 2.3.2.1). Sketches are, however, not totally accurate, being a semi-objective representation of the pelage pattern that is seen. Different observers may pick out different pattern components as being most salient. For instance if an animal has a patchy pattern roughly equal in dark and light components, one observer may sketch the white marks while another may sketch the dark marks. The high fidelity provided by photographic images was therefore the best way of identifying animals between observers and between years.

Extensive photographic work was carried out in 2001 founding the basis for this catalogue in addition to images captured previous to this study. The catalogue now contains around 350 entries. Each entry consists of the best full body and head and neck images available for each individual. Images were converted to greyscale format and reduced in size for easier storage and handling. Images were also altered using the 'adjust levels' and 'sharpen' tools in Adobe Photoshop 5LE to make the pelage patterns stand out as best as possible. It should be noted that the 'sharpen' tool alters the image by increasing contrast between light and dark areas, so making the pelage characteristics easier to distinguish but also making the image a less accurate representation of the animal. Each catalogue entry was prepared as a standardised Microsoft PowerPoint presentation including image data and other individual information (Figure 2.3.2.2).

### 2.3.3 Identification and matching using natural pelage markings

To assign identity either in the field or between photographs there must be a degree of certainty over which a decision can be accepted. This level of



Figure 2.3.2.1  
Example of a sketch used to identify animals

Name: Amie  
Mumno: 71001  
Location: S.EP-03  
Pup date: 11-10-03

Alias:  
Skin:

Images:

NR03IMG7535 NR03IMG7600  
NR03IMG8289  
NR03IMG6939 NR03IMG6883



Figure 2.3.2.2

Example of an identification catalogue entry

certainty is provided by the number of discrete bits of information used to make the decision. The larger the population from which two entities are to be matched, the more discrete bits of information should be used as it becomes more likely that two individuals may share certain characteristics. For instance, in a study of lions identified by vibrissae spot patterns it was calculated that 13 bits of discrete information were necessary to identify individuals at the 1% level from a population of 1000 (Pennycuick & Rudnai, 1970). Seal pelages, however, are much more difficult to quantify than the more uniformly structured array of lions' vibrissae. It would therefore be impossible to compute the probability of any pelage pattern arising and so the reliability of any identifications in any sample size. The advantage, however, is that while some aspects of a seal's pattern may be similar to that of another, each pelage pattern is unique. Also, grey seal pelage patterns often have highly complex components which can make individuals particularly distinctive. Although it is impossible to quantify confidence for this technique it is still possible and important to have a robust and structured protocol for the identification of individuals. All pelage components listed below can be identified and as many discrete bits of information as possible used to make a match so that a high level of certainty can be maintained.

1. Counter-shade line. Female grey seals often have a quite distinct primary counter-shading pattern over which the more complex spot pattern is overlaid. The position of the line delineating the darker dorsal surface with the lighter ventral surface is one bit of information. The contrast and shades of the countershading pattern constitute separate bits of information.

2. Permanent scars. Grey seals often have permanent scars such as bite wounds, flipper injuries and neck scars from fishing equipment. These should be distinguished from less permanent wounds which may not be present on re-identification. Again, the position *and* quality of feature are two separate bits of information. It must be noted that scars are gained over time and that there is a certain amount of temporal change of this feature.

3. Pattern components. The unique spot pattern present along the length of a grey seal's body is the most salient evidence of identity. Each pattern component can be differentiated by shape *and* position to provide multiple bits of information.

The ability to assign an identity to an image varies with both the quality of the image and the natural distinctiveness of the animal portrayed. In photo identification studies the biggest source of errors is non-matching due to poor quality images (Stevick et al., 2001). The photographic quality in this study was consistently very good. An animal that does not have a distinctive pelage may be more difficult to identify than one with a highly distinctive pelage. Primary areas for identification have historically been the head and neck. This is because pelage identification was initially carried out for animals at sea (Hiby & Lovell, 1990). In this study, however, the extent of imaging available for many seals allowed for any part of the body to be used for matching, particularly the flank. Even so, a small proportion of images do not provide enough information to make a match. This is unavoidable and can be caused by orientation or dirtiness of the animal, weather conditions, or the presence of obstacles between camera and animal. However, such instances were minimal (Table 2.3.1.1). Difficulty

may also arise in assignment of identity to both left and right sides of an animal. Due to the continuous nature of observations and the fact that images of both sides of most identified individuals within the study were known, this problem if present was minimal.

It is also worth noting that that many grey seals have patterns particularly distinctive to the human eye, such as those resembling a face or letter. These patterns, however, can be apparent on more than one seal and confusion may arise if too much attention is paid to these extra salient cues. It is very important then, especially in light of the above, to look at as much of the body as possible when confirming a match and not solely on what the eye is drawn to.

#### 2.3.4 Computer-aided matching

To check image matching both internally and with previously taken images, a selection of photographs were submitted for analysis by computer-aided matching as described in Hiby and Lovel (1990). Where possible, for each entry in the catalogue, a left and right head and neck image was submitted. The computer-aided matching procedure tests images in pairwise comparison with all others in the library. From these comparisons possible matches are generated to be confirmed by eye. For submission, images were converted to greyscale TIFF format files of 640 by 480 pixel resolution using Adobe Photoshop 5LE. This technique was initially developed for use on photographs of animals in the water. It therefore works best when photographs are of wet animals in a certain orientation. Such images are not typical of animals on the breeding colony and this presented difficulties to the matching program. Due to this and the

dependence on head and neck images only, computer aided matching was only used to a very limited extent in this study.

## 2.4 Behavioural observation

The maps produced from photo-identification surveys allowed the description of behaviour, specifically movement and the dynamics of association, on a coarse temporal scale. However, it was also necessary to describe fine-scale behaviour such as interactions and short term movement patterns. Where possible, after photo-identification surveys, the behaviour of animals within the study area was recorded. Due to a development of methodology, behavioural observations took different forms in 2002 and 2003.

### 2.4.1 Grey seal behaviour

Grey seal mothers on North Rona spend around 80% of their time ashore resting (Anderson & Harwood, 1985). When not resting, however, the predominant forms of non-breeding behaviour are involved in movement or antagonism. Antagonistic behaviour varies from an alert response to disturbance to fighting and chasing. Interactions can be broken down in scale of increasing intensity and decreasing frequency as follows.

1. Alert: Raise or turn head towards a disturbance.
2. Vocalisations, Open Mouth Threat (OMT) and clapping: Warning directed towards another in the form of vocalising in a howl or hiss, opening mouth, or clapping a fore-flipper against the flank.
3. Flipping and lunging: Direction of physical aggression by the fore-flipper or lunging of the head to bite, but no contact made.
4. Physical contact: The above when contact is made.
5. Prolonged fighting and chasing: When the above interactions are prolonged, repeated or pursuit is involved.

Interactions are typically short in duration. The median interaction duration recorded on Sable Island, Nova Scotia, was just 15 seconds (Boness et al., 1982). Each interaction may include a number of the above behaviours of which the highest intensity behaviour was always recorded.

#### 2.4.2 Behavioural observations in 2002

Approximately 25 hours of observations were carried out over 11 afternoons in the hours of daylight remaining after photo-identification scans. Within each observation period instantaneous scans of the study area were made at 5 minute intervals and the behaviour and position of each active female recorded. Positional information was recorded within a 10m grid provided by OSGB grid coordinates at a 10m resolution. Only interactions between females and between females and pups were recorded. Sexual behaviour was not a focus of this study and so interactions involving males were not recorded.

In addition to the above detailed continuous observations were made of groups of animals within the study area in 18 periods of 2 hours duration. During these periods the behaviour and location of each individual within the focal group being watched was recorded in real time.

#### 2.4.3 Behavioural observations in 2003

36 hours of observations were carried out in 3 hour periods during 12 afternoons after photo-identification scans. Within each observation period the entirety of the study area was observed and interactions were marked with meter accuracy on a map as they occurred. This enabled post hoc sampling of behavioural data to match the format of social stability data. Area based

estimates of social stability were calculated within a specific radius around grid cell centres (see Chapter 5), and so this was also possible for the behavioural data described here.

# **Chapter 3**

# **Behaviour**

### 3.1 Introduction

In order to appreciate and form hypotheses of animal sociality, it is first necessary to investigate general behavioural activity. Doing so provides the context within which sociality may operate. In grey seals the most common forms of non-maternal active behaviours are movement and aggression (Anderson & Harwood, 1985). These behaviours have fundamental implications for sociality. If movement is extensive then so will be the amount of mixing between individuals within the colony and so the number of other animals that an individual comes into contact with. If aggression is extensive then it would seem beneficial for an individual to reduce the number of others that it comes into contact with. It has been noted that mothers tend not to move great distances from their chosen pupping location (Anderson & Harwood, 1985) but that this movement can be affected by the availability of water (Redman et al., 2001). In addition, mothers tend to be more aggressive in the earlier stages of lactation (Boness et al., 1982). The primary aim of this chapter is to investigate the spatial scale over which movements and interactions take place. Only then is it possible to suggest a specific scale over which associations should be measured and so social structure be described. A spatial scale of association has been described previously for grey seals on North Rona. Redman (2002) argued that, within any one season, grey seal mothers infrequently move more than 10m from their initial pupping sites and as such females separated by more than 20m would be unlikely to interact. However, while Redman (2002) only sought to describe sociality between years, in this study it is also sought to investigate sociality within years. The scale over which short term sociality should be measured may differ to that over which long term sociality is measured. This is because

animals may be likely to move less and so come into contact with fewer others over a shorter time period. In addition, it was sought to confirm that the scale Redman (2002) used for investigating long term sociality was relevant to this study also.

Experimental manipulation is the most powerful tool available to scientists with which to examine specific hypotheses. Unfortunately it is notoriously difficult to carry out manipulations within wild populations. Here, an attempt was made to artificially control the social environment that animals within the colony experienced and note any resultant effect on behaviour.

## 3.2 Spatial scale of association

### 3.2.1 Inter-survey behaviour

Photographic surveys of the study area were undertaken throughout the 2002 and 2003 seasons as described in Chapter 2.3.1. As the identity and location of each individual within each survey was known it was possible to calculate the distances moved by each individual between surveys and throughout the season as a whole. The spatial scale over which animals operate, and so are likely to be able to interact, can therefore be calculated at the temporal resolutions over which sociality is measured.

To reduce the effect of possible influence on movement calculations by locations of animals in transit to or from their chosen pupping location at the beginning or end of lactation, the first and last coordinates at which each individual was observed were filtered. Coordinates were omitted from analysis if they were associated with a movement (to the next coordinate if an initial observation or from the previous coordinate if a final observation) greater than three times the average shown by that individual. In 2002 10 animals had one coordinate omitted and in 2003 18 animals had one coordinate omitted and one animal had two coordinates omitted.

#### Inter-survey movements

Figure 3.2.1.1 shows the median inter-survey movement distances for 54 mothers in 2002 and 66 mothers in 2003. The median distance moved was 2.87m in 2002 and 3.16m in 2003. This indicates that grey seal mothers on North Rona do not travel far. Indeed 98% of movements in 2002 and 97% of movements in 2003 were below 10m. From this it appears that, between surveys,

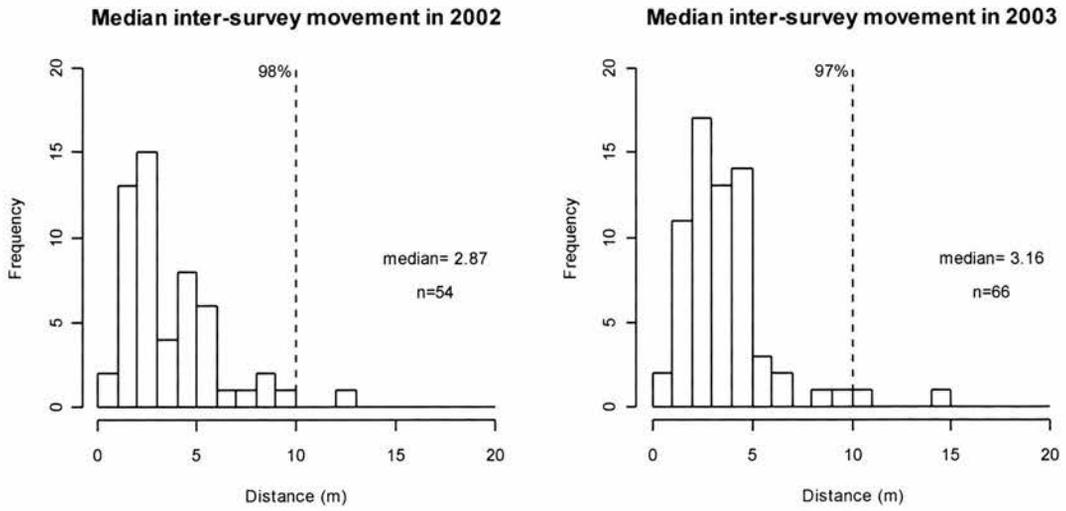


Figure 3.2.1.1 Median inter-survey movement distances for each resident mother in 2002 and 2003

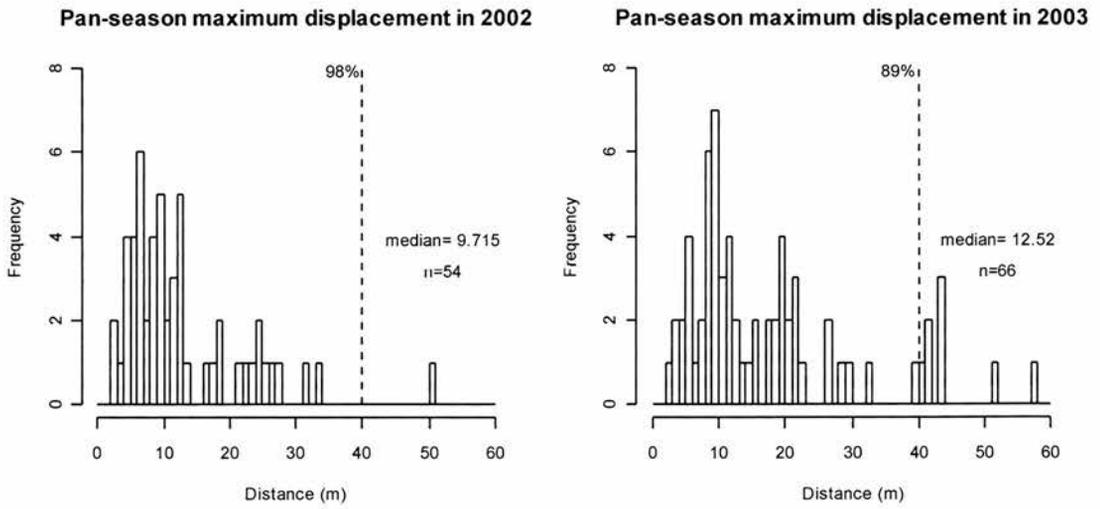


Figure 3.2.1.2 Maximum displacement distances for each resident mother in 2002 and 2003

an animal was unlikely to come into contact, and so be able to interact, with another that was more than 10m away.

### Pan-seasonal movement

The measurement of between year sociality was calculated with reference to a single location and date for each animal, summarising their residence on the colony (see Chapter 6). In order to provide a spatial scale of association for between year measurements it was therefore necessary to gauge the extent of movement by animals throughout their residence on the colony. Figure 3.2.1.2 shows the maximum displacement within the set of locations occupied by each resident mother in 2002 and 2003. The maximum displacement was calculated as the Euclidian distance separating points comprising the most extreme x and y coordinates that an animal occupied. The median maximum displacement was 9.72m in 2002 and 12.52m in 2003. 98% of animals had a maximum displacement less than 40m in 2002 and 89% in 2003. The maximum displacement of an animal's locations can be thought of as the diameter of a circle within which that animal has been observed to move. Animals were therefore not likely to move outwith a radius of 20m from their central location, and so would be unlikely to come into contact with others who are located more than 20m away.

### 3.2.2 Fine scale behaviour

Describing animal movement at the temporal scale over which social measurements are made is limited in usefulness if the behaviour of animals differs from that observed over a shorter time scale. It is therefore necessary to

examine animal behaviour at a time scale over which interactions and associations take place. In 2002 18 observation periods of two hours duration were undertaken in which the interactions and movements of each animal in predefined groups within the study area were recorded in real time. This allows analysis of the spatial scale of association at the most resolute of temporal scales and so provides a more accurate picture of which animals should be considered to be associated over both short and long time frames.

#### Animal movement

It appears that animals do not move more within a short time scale than observed between photographic surveys. The movement of 81 individuals is shown in figure 3.2.2.1. As some individuals were observed more than once, their median movement is provided to reduce any bias introduced by pseudo-replication. 'Net movement' describes the distance between the locations that each individual occupied at the start and end of each two hour observation period. The median net movement was 1.18m and animals only infrequently moved further than 10m. 'Path length' describes the gross distance that individuals actually travelled during the two hour period. Median path length was 3.73m so animals were likely to move further than their net movement would suggest. 'Maximum displacement' describes the distance between the most extreme positions that each individual occupied during the two hour period. The median maximum displacement was 1.96m. All three of these measures were highly skewed towards zero indicating that most individuals did not move far, if at all.

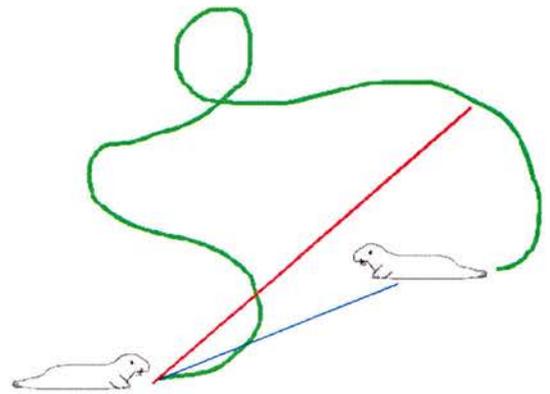
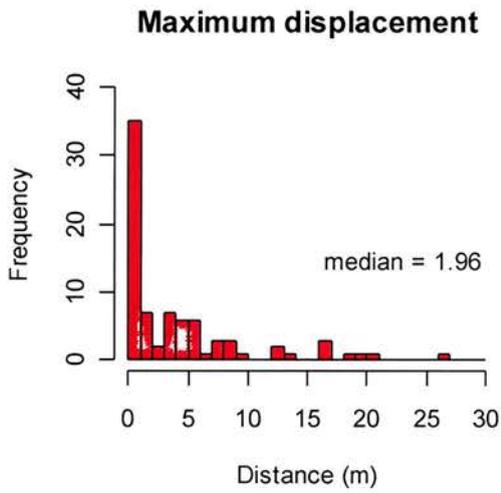
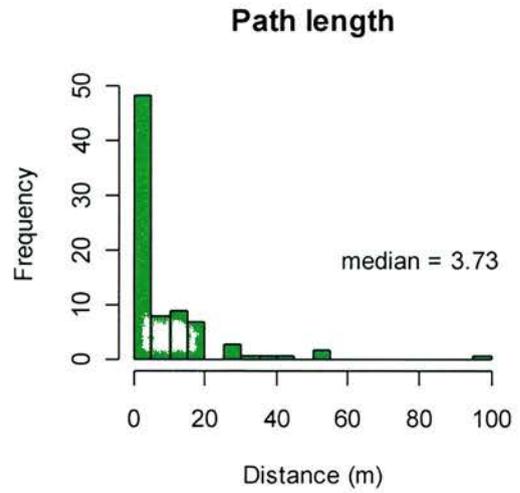
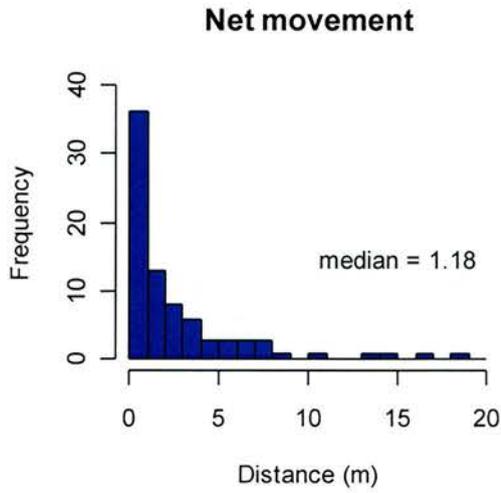


Figure 3.2.2.1 Net movement, path length and maximum displacement of 81 females observed over 18 two hour periods within the study area in 2002.

It was apparent that when movements did occur, they were generally non-directional and animals tended not to stray far from their original locations. Again, then, although individuals were capable of moving larger distances they were unlikely to stray farther than 10m from their initial position and so would be unlikely to interact with others outwith this range.

#### Interaction rates

The rates of interactions were very low for animals within the study area. Interaction rates were calculated as the number of interactions of level 2 or above (see Chapter 2) per female per hour. The two areas under study had mean interaction rates of 0.21 and 0.16. The difference between areas was not significant ( $t=0.62$ ,  $df=16$ ,  $p=0.54$ ). There was therefore only around a 20% chance that any female would be involved in an interaction every hour.

#### Separation distances between interacting animals

It was also possible to investigate the distances separating individuals that interacted within the observation periods. Figure 3.2.2.2 shows the distances that interacting individuals were separated by before, during and after each interaction. Interactions were of level 2 or above (see Chapter 2) and between females only. The 'initial separation' describes the distance separating animals at the start of the observation period that would subsequently interact. Repeated measures of initial separation for pairs of animals that interacted more than once were omitted. The 'pre-interaction separation' describes the distance separating interactants immediately preceding an interaction. This was recorded at the start of a 15min observation window in which the interaction took place. The 'during

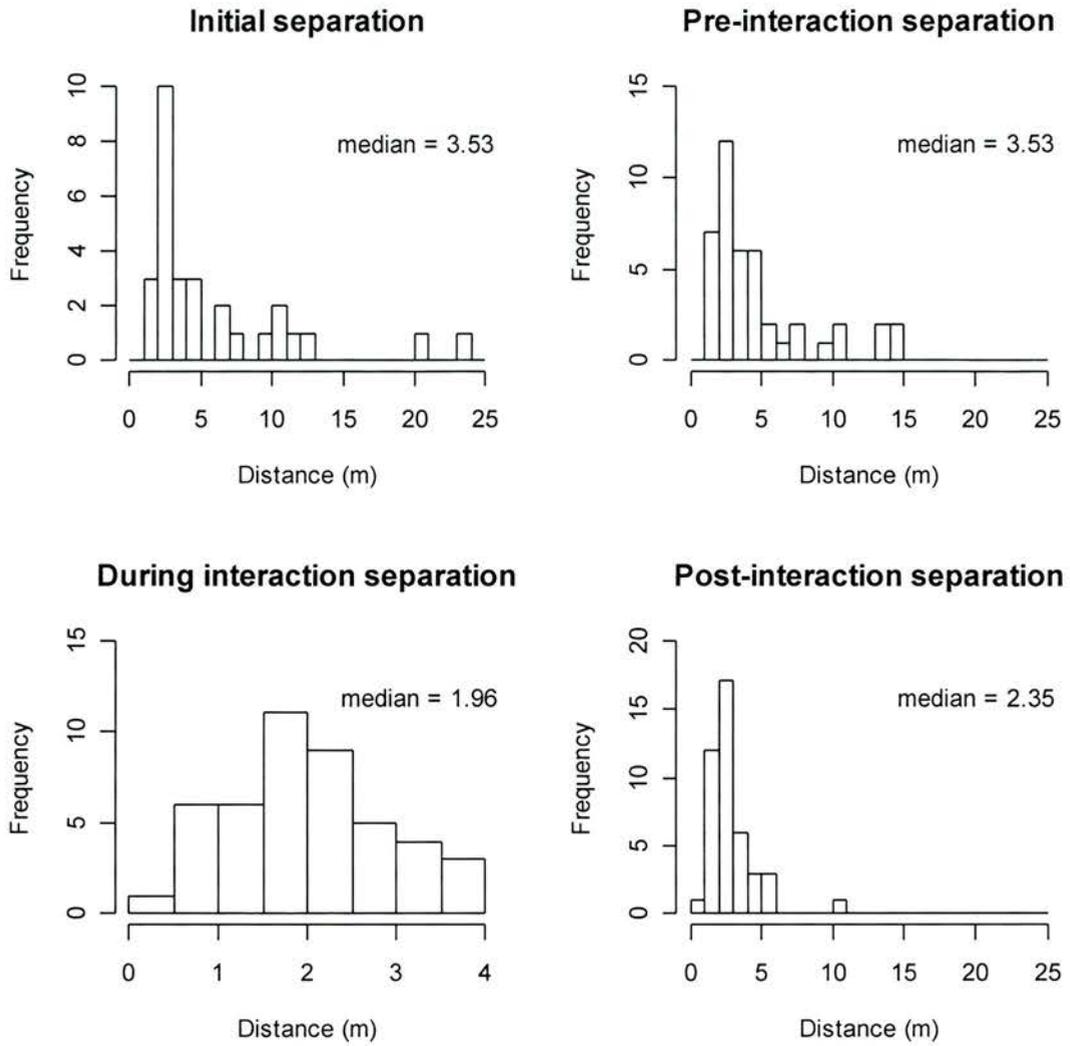
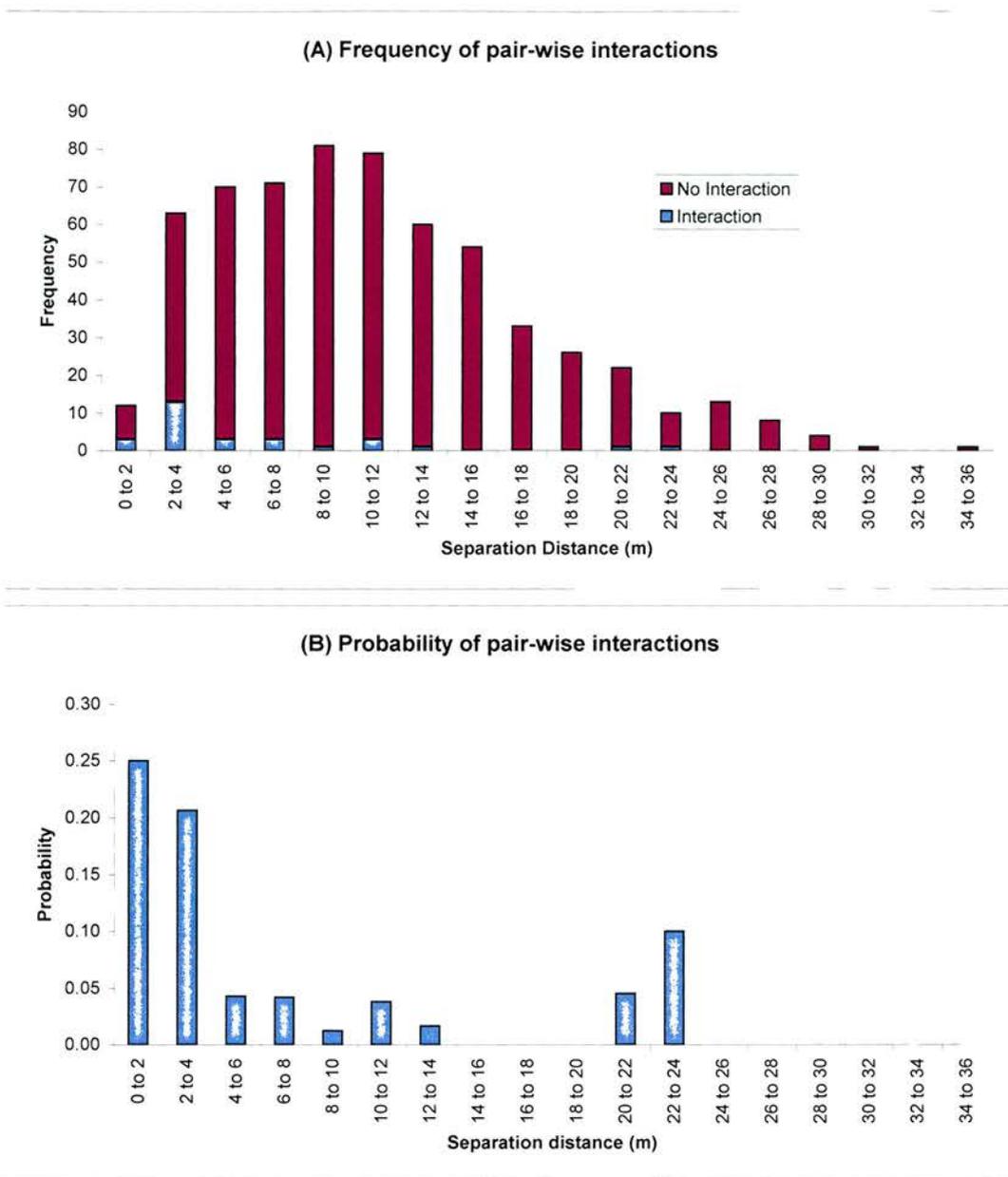


Figure 3.2.2.2 Distances separating pairs of interacting females. See text for details.

interaction separation' describes the closest distance separating the two interactants within the 15min observation window and so approximates to the distance over which the interaction took place. The 'post-interaction separation' describes the distance separating interactants immediately after the interaction took place, recorded at the end of the 15min observation window. It appears that animals were more likely to interact when they were closer together, and at distances predominantly less than 10m. Interactions took place over a few metres and interactants tended to be closer after an interaction than they had been before it.

#### Probability of interactions

Only a few animals in each focal group interacted within the two hour observation periods. It was possible to calculate the observed probability that animals separated by certain distances would subsequently interact. Figure 3.2.2.3(A) shows the frequency that animals separated by the given distances would subsequently interact or not. Figure 3.2.2.3(B) shows the probability that individuals separated by each distance class would subsequently interact. It is important to note that the total number of animals separated by larger distances in this data is inaccurate. In reality, the total number of animals separated by increasing distance should increase also. However, the observed totals appear to level off and start to fall after around 10m. This is because each focal group was not large enough to include all animals within distances greater than 10m for every individual. Therefore the apparently high probability of individuals separated by 20m to 24m is a misleading. In the range of accuracy provided by this data then, it appears that the probability of two animals interacting falls off



**Figure 3.2.2.3** Frequency and probability of pair-wise interactions  
 Note: data above 10m is unreliable (see text for details)

sharply as the separation distance increases to 10m. The probability that animals would interact if separated by more than 10m was very low.

### 3.3 Experimental manipulation

In 2003 the locations of two mothers and their pups were swapped. The two animals were initially separated by approximately 30m and so were considered to be within separate social groupings. Both animals were at similar stages, mid-way through lactation. Behavioural data was collected both before and after the swap and the expectation was for behaviour to change in relation to the change in social environment.

Unexpectedly, as soon as both animals regained mobility, after the sedation required during their capture had worn off, they began to return to their original positions. Initially, both animals were able to travel while maintaining contact with their pups. However, soon that contact was broken and both animals returned to their original positions, both without pups, within one and a half hours of immobilisation. After a further half hour, the pups were artificially returned to their mothers. The female-female interaction rate for both mothers in the morning preceding the swap was three interactions in three hours. In the afternoon following the swap, one animal was involved in two interactions and one in eight interactions in three hours. These interactions were, however, associated with movement of the mothers returning to their original positions rather than interacting with their new experimental associates. The directness of travel appeared quite remarkable. Although one of the mothers was deviated from her path when chased by a male, both returned to their original locations with little navigational difficulty. Even more remarkable, however, was that the stimulus to do this was apparently stronger than the stimulus to maintain contact with their pups. The instinctive bond between a mother and her pupping site

and/or associates therefore seemed stronger than the bond between a mother and her pup itself. The reasons why this may be are unclear.

### 3.4 Discussion

Interaction rates between female grey seals on North Rona were very low. The interaction rates of females at this site have previously been shown to be less than those within another Scottish colony on the Isle of May (Redman, 2002). In describing a spatial scale of association it is intended to offer a broadly applicable scale over which the behaviour of an animal is likely to impact others. Although interaction rates were low, movement patterns illustrate the distance over which animals are likely to come into contact with one another and so have such an impact. Individuals have been shown to move predominantly within 10m, both at medium and fine-scale temporal resolutions. In addition, when interactions do occur, these are most likely between individuals separated by less than 10m. It is likely then, that in the short term, animals were likely to come into contact with others less than 10m away, but were unlikely to come into contact with those at a distance greater than 10m. A spatial scale of 10m therefore appears to be a useful one within which to measure short to medium term sociality. However, behaviour over the entire season suggests that animals may come into contact with others over greater distances. It is likely that animals are able to come into contact with others within a range of 20m over their entire period of residence. Redman's (2002) scale of 20m, around a central summary location, is therefore supported for calculations of sociality between breeding seasons.

Interestingly, after an interaction, mothers did not appear to separate to a great degree but remained closer together than before the interaction had taken place. On a study of animals on Sable Island, Nova Scotia, however, Boness et al. (1985) observed that an aggressive interaction would most likely result in an

increase of distance between the interacting individuals. On North Rona, it is often very difficult to assign an outcome in terms of winners and losers to interactions between females because there is rarely a clear retreat or submission by either individual (pers. obs.). Interactions do occasionally lead to physical injury and may also be involved in increased levels of stress or breakage of the mother-pup bond, one of the most likely factors influencing pup mortality (Anderson et al., 1979). Although infrequent then, the effects of interactions may on occasion be catastrophic. On most occasions, interactions do seem effective in protecting a mother and pup's immediate personal space.

When individuals were removed from their chosen locations and social groups they returned to them with remarkable speed and accuracy. Although this is a case study, it appears that the instinct of mothers to do this appeared stronger than the instinct to maintain contact with their pups. Breakage of the mother-pup bond is the single most contributory factor to pup mortality so the apparent frailty of this bond is surprising (Anderson et al., 1979). Mothers are also quite frequently seen to protect the placenta (particularly from gulls) better than they do their pups (pers. obs.). The reasons as to why this may be are not clear. Perhaps the bond between a mother and her pup is less developed than in other species. After all, maternal instinct must be curtailed very sharply at weaning when the mother abruptly abandons her pup, leaving to mate and return to the sea. In light of this, researchers must be very careful during any future disturbance of these animals, and be acutely aware of the dangers involved in separating mothers and pups.

# **Chapter 4**

## **Measuring sociality**

#### 4.1 Introduction

Sociality is a most influential part of any species' life history in both shaping and being subject to the selective pressures and evolutionary opportunities that mould a species to its current form. Intra-specific variation in social behaviour may therefore be a particularly potent measure, having repercussions for individual fitness and so in turn evolutionary development. This can take place on many scales, forms of sociality ranging from loose and ephemeral aggregations to complex and intricate relationships made up themselves of series of component interactions (Hinde, 1976). Most animals must socialise, if only for the purpose of reproduction. Even those which spend most of their adult life in solitude, for instance male tigers (*Panthera tigris*) and giant pandas (*Ailuropoda melanoleuca*), must meet conspecifics for mating events (Miquelle, 2001; Zhi, 2001). Patchy distribution of resources can also cause otherwise solitary animals to aggregate, for instance polar bears (*Ursus arctos*) aggregating around a dead whale to feed (Stirling, 2001). In comparison, the complex social systems of the eusocial insects bind individuals to a life spent constantly working for the benefit of others, and of course through inclusive fitness, for themselves (Manning & Dawkins, 1998; Slater, 1999). Even at the bottom of the scale of social complexity reciprocity and conflict reduction have the potential to provide benefits to participating individuals (Axelrod & Hamilton, 1981).

The measurement of sociality is very important to understanding its role in animal life histories and the contexts in which sociality is promoted. Appropriate measurement must take a form suitable to the context in which it is being carried out and the type of information required from such a measurement

may be different for each circumstance in which it is employed. Hinde (1976) set out a framework for the study of sociality in which he proposed three main levels. Here, behavioural 'interactions' underpin the formation of 'relationships' between specific individuals and the network of such pair-wise relationships forms the overall 'social structure' of a system. Much work has been carried out describing social structure using a bottom-up approach, by measuring interactions to form an overall picture of the relationship network. Of course, interactions are not always easy to observe and in many circumstances a proxy such as group membership or spatial and temporal separation distance are used, being prerequisites for overt behavioural interaction (Whitehead & Dufault, 1999). When even this is difficult to observe measures such as home range overlap or coordinated movement may be used (Poole, 1995). Such work is common in the study of fission-fusion societies and has been carried out on a wide range of species (for instance: sperm whales, *Physeter macrocephalus* (Whitehead et al., 1991), bottlenose dolphins, *Tursiops aduncus* (Chilvers & Corkeron, 2002; Quintana-Rizzo & Wells, 2001), cattle, *Bos taurus* (Lazo, 1994), American bison, *Bison bison* (Lott & Minta, 1983), eland, *Taurotragus oryx* (Underwood, 1981), vampire bats, *Desmodus rotundus* (Wilkinson, 1985), and sanderlings, *Calidris alba* (Myers, 1983)). Much of this work employs the use of pair-wise association indices (for more examples and a review see Whitehead and Dufault (1999)). These typically provide a proportion of observations in which two individuals are seen together. The more frequently two individuals are observed together, the stronger their association index and so the closer they would be placed in a representation of the social structure. This social structure can be represented using a variety of techniques such as cluster

analysis, multidimensional scaling or sociograms (Whitehead & Dufault, 1999). There are a variety of association indices that a researcher can choose from which, although closely related, have slightly different properties. It is therefore important that an index is chosen to suit the study in question (Cairns & Schwager, 1987; Ginsberg & Young, 1992).

Female grey seals colonise North Rona every autumn to breed (Anderson et al., 1975). In contrast to the studies outlined above, this provides the primary window of opportunity in which detailed quantification of breeding and social behaviour can be made. In addition, measurements of reproductive performance allow the quantification of breeding success and so investigation of the effect that social behaviour may have on animal fitness. Although socially gregarious, female grey seals are not known to engage in cooperative behaviours. Any social organisation within the colony is therefore likely to be at a low level. The focus of this study is to assess how the social environment may affect breeding female grey seals. There are two main reasons why traditional measures of pair-wise association are unsuited to this task. Firstly, pair-wise measures assume free mixing of individuals within the population being studied. That is, sampled individuals should be fully independent, having the opportunity to associate with any other in the population irrespective of who they have associated with previously. However, within seasons, grey seal mothers breeding on North Rona do not adhere to this assumption. Mothers typically do not move more than 10m in any one day and stay close to their pupping location (Chapter 2). As such it is more likely that an individual will be associated in subsequent samples with those that it has already been associated with in previous samples, barring influx and efflux to the colony. A grey seal colony can certainly be described as

dynamic but not as free mixing. The second reason that traditional pair-wise methods are inappropriate could be described as one of focus. Traditional methods are concerned with measuring social behaviour at the most resolute of scales, quantifying the 'interactions' of Hinde's (1976) framework to elucidate pair-wise 'relationships' and so infer overall 'social structure'. Interaction rates between grey seal mothers on North Rona are very low (Chapter 2). Grey seal mothers are not involved in any overt cooperative behaviours and the advantage of sociality hypothesised in this system is, if anything, of conflict reduction through familiarity afforded by stability in the social environment. As such the detail of pair-wise associations would both be very difficult to accurately quantify and also provide information at a scale that does not match that of the hypothesis. Rather, it is required to quantify that stability in the social environment directly. The aim of this chapter is therefore to define a suitable environmental measure of social change. Such a measure should be applicable within a spatial context through time, either in a particular area or around a particular individual and either from one day to another, across the breeding season as a whole or between breeding seasons. In this way it will be possible to describe the social stability that areas on the grey seal breeding colony present and the social stability that individuals within the colony actually experience.

## 4.2 Similarity coefficients and beta-diversity measures

### 4.2.1 Measuring similarity

As detailed above, the aim of this chapter is to provide an environmental measure of social change. To formulate the mathematical requirements of such a measurement it is best to think in terms of lists. The social makeup of the colony, or any subsection of it, at any particular time can be described by a list of all individuals present at that time. Social change, then, can be described by differences between such lists. Complication arises as this study is not concerned simply with differences in size between lists but with differences in composition. There is a wealth of literature from various disciplines concerned with the quantification of differences, or similarities, between lists (for instance in genetics, e.g. (Fu et al., 2003; Lynch, 1990), linguistics, e.g. (Lame, 2001; Och & Ney, 2003) and ecology, e.g. (Koleff et al., 2003; Magurran, 2003)). Quantitative assessments of change are computed using a variety of similarity coefficients or beta-diversity indices. As Southwood (1978) warns, however, such quantification is not as intuitively undemanding as it initially appears. There are no examples that the author is aware of utilising existing procedures for the purposes intended here and it would seem advisable to be careful when adopting a procedure devised for one particular purpose and using it for another. Existing measures of change may behave unfavourably when used in contexts other than that they were created for and so care must be taken to ensure that any use of such measures is appropriate. It is therefore of utmost importance to scrutinise existing measures thoroughly before application to this particular context. Below I describe a variety of such measures before subjecting them to

test in order to choose which may be suitable for use in quantifying changes through time in the social environment.

#### 4.2.2 Ecological diversity

Many investigators have been concerned with the measurement of ecological diversity. That is, the richness or otherwise of species and how this differs over various spatial and temporal scales (see Magurran, 2003). There are three main types of diversity measured in ecology:

1. Alpha diversity is concerned with the diversity of species within a sample (eg. habitat) and can be influenced by the abundance of each species within that sample.
2. Beta diversity is concerned with the difference in diversity between samples (of alpha diversity) within the overall diversity of a landscape.
3. Gamma diversity is concerned with the diversity of species within all samples (eg. in a landscape made up of a variety of habitats).

Work has primarily concentrated on measuring diversity across geographic or habitat gradients, e.g. (Harrison et al., 1992; Routledge, 1977), but it has been noted that the same techniques are equally applicable to measuring diversity through time, and indeed this has been done (Rodrigues et al., 2000; Russell et al., 1995). Beta diversity has also been referred to as turnover and in the case of measuring change over time this seems particularly apt. (Note that "true turnover" in the literature refers to species replacement rather than simply change which could also include species loss or gain (Harrison et al., 1992)). In the context of this study where I am concerned with measuring the change in

composition between lists of individuals present at successive time points the above definitions can be amended as follows:

1. Alpha diversity: the number of individuals at a particular time point
2. Beta diversity / turnover: the change in individuals between time points
3. Gamma diversity: the number of individuals across all time points (within season)

It can be seen from the above that both alpha and gamma diversity are described in their most simple forms by the number of individuals (or species) present within the appropriate spatial or temporal resolution. As with measuring beta diversity there are various algorithms available with which to measure alpha and gamma diversity that take into account the abundance of each species present (see (Magurran, 2003; Southwood, 1978)). In the context of this study, however, the abundance of any entry on a list can only ever be 1 as each entry represents a single individual. The simplest measure of diversity is therefore the number of individuals present within (alpha) or across (gamma) samples. To aid in comparison of the following indices I shall, where possible, present each formula according to the standard symbology below:

- $a$  - the number of individuals present at both of two time points  
i.e. the number of shared entries on both list 1 and list 2
- $b$  - the number of individuals present only at the first of two time points  
i.e. the number of entries unique to list 1
- $c$  - the number of individuals present only at the second of two time points  
i.e. the number of entries unique to list 2
- $s$  - alpha, the total number of individuals present at one time point  
i.e. the total number of entries on a list
- $S$  - gamma, the total number of individuals present across all time points  
i.e. the total number of unique entries from all lists
- $N$  - the total number of time points  
i.e. the number of lists

Note that under these rules when  $N = 2$ , for the first of two time points  $s$  could be expressed as  $a + b$  and for the second of two time points as  $a + c$ . Similarly,  $S$  could be expressed as  $a + b + c$ . The sum total number of entries over both time points is equal to  $2a + b + c$ .

#### 4.2.3 Indices for pair-wise comparisons

The following indices are concerned with measuring the difference between two lists only. In the context of this study these indices relate to change between two discrete time points but not across multiple time points such as the entire breeding season. Information about change across the season as a whole must therefore be calculated as a summary statistic such as the mean or median over all time steps. This may appear less ideal than indices which measure

change across the whole season, however they are advantaged in being intuitively simple.

### 1. Dice Coefficient (SSd)

One of the most popular algorithms for computing ecological beta diversity is the Dice coefficient (Dice, 1945). This is also known as the Sorensen, Czekanowski or Bray-Curtis presence-absence measure of beta diversity (Magurran, 2003; Southwood, 1978). Using the symbology above this can be written as:

$$SSd = 2a / 2a + b + c$$

This describes the proportion of sum total entries that are shared between two lists, or in the context of this study, the proportion of the sum total of individuals that are present at both of two time points. The output can take values from 0 indicating no similarity between the two lists to 1 indicating that the two lists are identical. If this is a measure of similarity then its complementary form is a measure of dissimilarity. Russell's (1995) measure of turnover can be expressed as:

$$b + c / 2a + b + c$$

which is effectively the same as:

$$1 - (2a / 2a + b + c)$$

This can be treated as having the same properties, although in reverse, as the Dice index.

2. Jaccard Coefficient (SSj)

Another popular algorithm is the Jaccard Coefficient which takes the form:

$$SSj = a / a + b + c$$

This appears very similar to the Dice coefficient other than the weighting given to  $a$ . The difference lies in the denominator which in the Dice coefficient is equal to the sum total number of individuals encountered at both time points. The denominator of the Jaccard coefficient, however, is equal to the total number of unique individuals encountered at both time points. The Jaccard coefficient therefore calculates the proportion of all individuals encountered from time 1 to time 2 that are present at both time 1 and time 2 (Southwood, 1978). Again, this index can take values of 0 indicating no similarity between lists to 1 indicating that both lists are identical. A complementary form of the Jaccard index is called the Marczewski-Steinhaus index (Magurran, 2003).

3. Simpson's measure of Beta Diversity (SSs)

This index is similar to the complement of the Jaccard index, but the denominator takes the value of the total of the smallest of the two lists being compared:

$$SSs = 1 - (a / a + \min(b,c))$$

This reduces the effect of large differences in total number of entries between the two lists (Magurran, 2003). It can take values of 0, indicating that both lists are identical (no diversity) to 1, indicating no similarity between the lists (maximum diversity).

4. Social Cohesion (SSsc)

The indices described in this chapter range from the simple and intuitive to the complex and abstract. Simple measures are often the best for many reasons not least of which is transparency (Magurran, 2003; Southwood, 1978). The most simple measure to describe change in composition between lists takes the form:

$$SSsc = a / (a + b)$$

This index describes the proportion of all individuals present at the first time point that are also present at the second time point. This formula has been presented before in the ecological literature (Ruggiero et al., 1998). The difference between this measure and the Dice and Jaccard coefficients presented above is that the total number of individuals present at the second time point do not affect the output (other than a being a component of the total at the second time point). The result of this is where the Jaccard and Dice coefficients are diluted by new individuals present at the second time point this measure is not, being concerned only with the re-occurrence of individuals from the first. For this reason and in the context of this study this measure will be referred to as the index of Social Cohesion. It is, of course, clear that new animals present at the second time point are affecting the social change which it is sought to quantify and so it would be inadvisable to ignore them completely. In calculating Social Cohesion along a time series, however, the behaviour of any new animals at one time point are quantified in the proceeding time step. That is, if these new individuals remain overall Social Cohesion will be inflated, whereas if they leave overall Social Cohesion will be deflated.

5. Tripartite Similarity Index (SSt)

Tulloss (1997) reviews and assesses various similarity indices and highlights problems associated with each. He suggests a new approach for summarising the similarity between two lists using a set of cost function algorithms. These cost functions express, mathematically, a series of rewards or penalties based on the requirements of similarity made explicit by the user. The product of these cost functions then provides an output metric analogous to an index value. Tulloss made explicit three principal requirements that a similarity index should be sensitive to:

1. the relative difference in size between two lists. This was addressed by the following algorithm which provides increasing penalty to lists of increasing difference in size.

$$U = \text{LOG}_{10}(1 + ((\min(b,c) + a) / (\max(b,c) + a))) / \text{LOG}_{10}(2)$$

2. the relative difference in size between the smallest list and the list of shared entries. This was addressed by the following algorithm providing increasing penalty for increasing difference in size:

$$S = 1 / (\text{SQRT}(\text{LOG}_{10}(2 + (\min(b,c) / (a + 1)))) / \text{LOG}_{10}(2))$$

3. the percentage of both lists that are shared between lists. This was addressed by the following function providing a reward for increasing percentage of shared entries between lists:

$$R = (\text{LOG}_{10}(1 + (a / (c + a))) * \text{LOG}_{10}(1 + (a / (a + b)))) / ((\text{LOG}_{10}(2) * \text{LOG}_{10}(2)))$$

The Tripartite Similarity Index value can then be calculated by:

$$T = \text{SQRT}(U*S*R)$$

This value ranges between 0, indicating no similarity between lists, to 1, indicating that the two lists are identical. Tulloss recommended this method as being suitably invariant (T does not vary significantly with inputs of varying size but similar composition) and linear (T varies consistently with changes in the list of shared entries). It is, however, both abstract and unwieldy.

#### 4.2.4 Indices for multiple comparisons

The following indices have an advantage over the previous in being applicable to a series of time steps and not just one. They can, of course, be calculated over just two time points (one time step), in which case being comparable to the similarity coefficients above, but have the added utility of providing a single value for multiple comparisons.

#### 6. Jaccard Coefficient Adapted for Multiple Samples (SSmj)

The Jaccard Coefficient has been adapted to provide a single measure across a series of samples (Colwell & Coddington, 1994) such that:

$$SSmj = \sum U_{jk} / N$$

Here,  $U_{jk} = S_j + S_k - 2V_{jk}$ .  $S_j$ , using the notation of this study, translates to  $s$  (number of individuals) at time point  $j$  and  $S_k$  to  $s$  at time point  $k$ .  $V_{jk}$  represents the number of individuals present at both time point  $j$  and time point  $k$ , and so is equivalent to  $a$ . Given that the total number of entries on two lists ( $S_j + S_k$ ) is equal to  $2a + b + c$  (see above) the formula can be re-written as:

$$\sum(2a_i + b_i + c_i - 2a_i) / N$$

which is the same as:

$$\sum(b_i + c_i) / N$$

where  $i$  is one time step in series  $N$ . Magurran states that when  $N$  is large this index approaches the value  $S/4$ . This index takes values of 0 when all individuals at all time points are unique and increases as increasing numbers of individuals stay constant across time points.

7. Whittaker's measure of Beta Diversity (SSw)

This simple formula is calculated by:

$$SSw = S / \text{mean}(s)$$

and equates to the proportion by which the total number of individuals across all time points is greater than the mean number of individuals at each time point (Whittaker, 1960). This ranges between 1, indicating that all samples are identical, to a maximum of  $N$ , indicating every sample is unique. When  $N$  is 2, 1 can be subtracted from the index to provide a range of 0 to 1 (Magurran, 2003). When this is done, it appears that Whittaker's measure is equal to the complement of the Dice coefficient:

$$\begin{aligned} \frac{S}{\text{mean}(s)} - 1 &= \frac{a + b + c}{(2a + b + c) / 2} - 1 = \frac{2(a + b + c) - 1}{2a + b + c} \\ &= \frac{2a + 2b + 2c - 2a - b - c}{2a + b + c} = \frac{b + c}{2a + b + c} = 1 - \frac{2a}{2a + b + c} \end{aligned}$$

8. Harrison's First Measure of Beta Diversity (SSh1)

Harrison et al. (1992) noted that Whittaker's index lacked the ability to be compared over series of different length ( $N$ ). They provided the following adaptation to correct for this:

$$SSh1 = (((S / \text{mean}(s)) - 1) / (N - 1)) * 100$$

Here, Whittaker's scaled measure is divided by the number of time steps involved and multiplied by 100. This index now ranges between 0 and 100, but could of course easily be adapted to range between 0 and 1.

#### 9. Harrison's Second Measure of Beta Diversity

Harrison et al. (1992) also noted that Whittaker's measure could be affected by successive variation in  $s$ . To address this the following formula was devised:

$$SSh2 = (((S / \max(s)) - 1) / (N - 1)) * 100$$

This calculates the amount by which the total number of individuals across all time points is greater than the maximum number of individuals from all time points. Again, this measure ranges between 0 and 100.

#### 10. Cody's Measure of Beta Diversity (SSc)

Cody (see Magurran, 2003) proposed an intuitively simple measure based on the number of individuals gained and the number lost across all samples. This can not be expressed neatly with the notation used so far and so the equation:

$$SSc = (\text{gained} + \text{lost}) / 2$$

refers to the mean of the number of individuals gained when moving in progression along a series of samples and the number of individuals that are lost along the series. It is worth noting that this is an additive process taking into account all samples along the series and not just those at the extreme ends. The output ranges from 0, indicating that no individuals are gained or lost and so all samples are identical, and increases as the mean number of gained plus lost individuals increases.

11. Wilson and Shmida's Measure of Beta Diversity (SSws)

Wilson and Shmida (1984) reviewed a selection of beta diversity measures, assessing their behaviour in relation to four criteria: providing a meaningful measure, additivity, independence from variation in  $s$  and independence from sample size,  $S$ . In conclusion they supported the use of Whittaker's (1960) measure and also one of their own. This combines aspects of both Cody's and Whittaker's measures of beta diversity such that:

$$SSws = (\text{gained} + \text{lost}) / 2 * \text{mean}(s)$$

This standardises gain and loss of individuals across samples by the mean number of individuals within samples. To further illustrate the inter-relation of these indices it is worth noting that over two time points this measure is the same as the complementary forms of the Dice index. As when  $N=2$ , the number of animals lost is equal to  $b$  and the number of animals gained is equal to  $c$ :

$$\frac{\text{gained} + \text{lost}}{2 * \text{mean}(s)} = \frac{b + c}{2 * (2a + b + c) / 2} = \frac{b + c}{2a + b + c} = 1 - \frac{2a}{2a + b + c}$$

12. Routledge's I Measure of Beta Diversity (SSr)

Wilson and Shmida (1984) also present an adaptation of a process devised by Routledge (1977) which is based on the principles of information theory. This adaptation is a simplification of the original for use with presence and absence data rather than abundances. This takes the form:

$$SSr = LN(T) - ((1/T) * \sum_i (e_i * LN e_i)) - ((1/T) * \sum_j (s_j * LN s_j))$$

where  $e_i$  is the number of time points at which individual  $i$  is present,  $s_j$  is the number of individuals present at time point  $j$  and  $T = \sum_i (e_i) = \sum_j (s_j)$ .

#### 4.2.5 Problems with indices

Even before testing it is clear that indices, as derived variables, are not without their problems. For instance, the Dice index is commonly used in genetic studies as the band-sharing coefficient to quantify similarity between two genetic samples based on the bands produced during gel electrophoresis (Fu et al., 2003; Leonard et al., 1999; Lynch, 1990). This is calculated as the number of bands shared between two samples divided by the mean total number of bands in each sample. Note that the denominator in this form is composed of the mean total number of bands from each sample. This highlights a problem known in engineering as 'aliasing'. Aliasing particularises the situation when an index can produce the same output for a variety of inputs (Tulloss, 1997). Here, it is apparent that the mean of two totals could be the result of many different combinations of totals. The result is that information is lost about any difference in size between the two totals.

Another problem, but one that is common to all indices, is increasing discreteness of the output when the denominator is small (Sokal & Rohlf, 1994). For instance, under the Dice index, if there are only two individuals present at each time point (and so total 1 + total 2, or  $2a + b + c = 4$ ), then  $a$  can only be 0, 1 or 2 and the index can only take values of:

$$(2*0)/4 = \underline{0}, (2*1)/4 = \underline{0.5} \text{ or } (2*2)/4 = \underline{1}$$

If, however, there were ten individuals at each time point the index could take many more values:

$$(2*0)/20 = \underline{0}, (2*1)/20 = \underline{0.1}, (2*2)/20 = \underline{0.2}, (2*3)/20 = \underline{0.3}, \text{ etc...}, (2*10)/20 = \underline{1}$$

One result of this is that given fewer animals the behaviour of each individual will have more impact on the index value. It could be argued whether or not this

has any biological significance. For instance, the impact that one animal's behaviour has on another may or may not be diluted by the presence of other animals. In the case of this study, it is assumed that environmental social change is more important than specific pair-wise interactions and so this should not be a problem.

### 4.3 Indices Tested

To better understand the properties of the above indices it is necessary to observe their behaviour in operation. The properties required of a similarity index will vary from study to study and it is important to make sure that any index used is behaving in the appropriate manner. The following properties are required in this study:

1. Transparent and intuitive
2. Independence from  $S$ , the number of individuals
3. Independence from  $N$ , the number of time points

A series of data sets have been constructed to test how each index behaves under certain circumstances and whether or not they conform to the requirements above. The first data set comprises ten individuals present at time 1 and ten individuals present at time 2. Five of these individuals are present at both times 1 and 2 (Table 4.3.1). This can be thought of as the standard data set to which the test data sets can be compared.

Tests 1 and 2 are concerned with how the indices perform at the extremes of change, that is no change at all or complete change in the presence of individuals between time points. A well performing index is expected to range between an intuitive minimum and maximum. Tests 3 to 8 illustrate how sensitive the indices are to small and large changes in  $s$  between time points. In test 3 there is 1 more emigration than the standard data set and in test 4 there is one more immigration. In test 5 there is no immigration and in test 6 there is no emigration. In test 7 there is large scale emigration and in test 8 there is large scale immigration. Tests 9 and 10 are composed of the same patterns of change as the standard data set but different numbers of individuals. This will show if

Table 4.3.1. Tests of social indices (1 to 13)  
See text for details. Red / blue colour indicates higher / lower similarity than standard test.

	Standard	1. All same	2. All change	3. 1 more emigrate	4. 1 more emigrate	5. 5 emigrate	6. 5 emigrate	7. 95 emigrate	8. 95 emigrate	9. More emigrate	10. Less animals	11. More Time	12. 5 then 6	13. 7 then 8
s1	10	10	10	10	10	15	5	100	10	20	4	10	15	10
a1	5	10	0	5	5	5	5	5	5	10	2	5	5	5
b1	5	0	10	5	5	10	0	95	5	10	2	5	10	5
c1	5	0	10	4	6	0	10	5	95	10	2	5	0	95
s2	10	10	10	9	11	5	15	10	100	20	4	10	5	100
a2	-	-	-	-	-	-	-	-	-	-	-	5	5	5
b2	-	-	-	-	-	-	-	-	-	-	-	5	0	95
c2	-	-	-	-	-	-	-	-	-	-	-	5	10	5
s3	-	-	-	-	-	-	-	-	-	-	-	10	15	10
S	15	10	20	14	16	15	15	105	105	30	6	20	25	110
N	2	2	2	2	2	2	2	2	2	2	2	3	3	3
SSt: U1	1.00	1.00	1.00	0.93	0.93	0.42	0.42	0.14	0.14	1.00	1.00	1.00	0.42	0.14
SSt: S1	0.82	1.00	0.53	0.84	0.82	1.00	1.00	0.82	0.82	0.81	0.84	0.82	1.00	0.82
SSt: R1	0.34	1.00	0.00	0.37	0.32	0.42	0.42	0.04	0.04	0.34	0.34	0.34	0.42	0.04
SSt: U2	-	-	-	-	-	-	-	-	-	-	-	1.00	0.42	0.14
SSt: S2	-	-	-	-	-	-	-	-	-	-	-	0.82	1.00	0.82
SSt: R2	-	-	-	-	-	-	-	-	-	-	-	0.34	0.42	0.04
SSr: T	20	20	20	19	21	20	20	110	110	40	8	30	35	120
SSr: $\sum(ei*LNei)$	6.93	13.86	0.00	6.93	6.93	6.93	6.93	6.93	6.93	13.86	2.77	16.48	89.29	16.48
SSr: $\sum(sj*LNsj)$	46.05	46.05	46.05	42.80	49.40	48.67	48.67	483.54	483.54	119.83	11.09	69.08	16.48	506.57
1. SSd	0.50	1.00	0.00	0.53	0.48	0.50	0.50	0.09	0.09	0.50	0.50	mean=	0.50	mean=
2. SSj	0.33	1.00	0.00	0.36	0.31	0.33	0.33	0.05	0.05	0.33	0.33	mean=	0.33	mean=
3. SSs	0.50	1.00	1.00	0.44	0.50	0.00	0.00	0.50	0.50	0.50	0.50	mean=	0.50	mean=
4. SSsc	0.50	1.00	0.00	0.50	0.50	0.33	1.00	0.05	0.50	0.50	0.50	mean=	0.50	mean=
5. SSst	0.53	1.00	0.00	0.54	0.49	0.42	0.42	0.07	0.07	0.53	0.54	mean=	0.42	mean=
6. SSmj	5.00	0.00	10.00	4.50	5.50	5.00	5.00	50.00	50.00	10.00	2.00	6.67	6.67	66.67
7. SSw	1.50	1.00	2.00	1.47	1.52	1.50	1.50	1.91	1.91	1.50	1.50	2.00	2.14	2.75
8. SSH1	50.00	0.00	100.00	47.37	52.38	50.00	50.00	90.91	90.91	50.00	50.00	50.00	57.14	87.50
9. SSH2	50.00	0.00	100.00	40.00	45.45	0.00	0.00	5.00	5.00	50.00	50.00	50.00	33.33	5.00
10. SSsc	5.00	0.00	10.00	4.50	5.50	5.00	5.00	50.00	50.00	10.00	2.00	10.00	10.00	100.00
11. SSws	0.50	0.00	1.00	0.47	0.52	0.50	0.50	0.91	0.91	0.50	0.50	1.00	0.86	2.50
12. SSr	0.35	0.00	0.69	0.33	0.36	0.22	0.22	0.24	0.24	0.35	0.35	0.55	0.53	0.43

the indices are independent of  $S$  and so comparable over data series of differing numbers of animals. Test 11 is composed of the same pattern of change but over one further time step. This will illustrate if the indices are independent of  $N$  and so comparable for data series of differing lengths. Test 12 can be thought of as test 5 followed by test 6 and will illustrate how each index summarizes the occurrence of these two different scenarios. Test 13 can be thought of as test 7 followed by test 8 and will illustrate how the indices behave with both one extra time step and successive variation in  $s$ . The required parameters and resultant index outputs for each of these tests are shown in Table 4.3.1.

It is evident from Table 4.3.1 that some of the indices violate one or more of the requirements outlined above. The Tripartite, Cody and Multiple Jaccard measures are all affected by  $S$ , the number of individuals sampled (tests 9 + 10). As this study requires the comparison of social change over samples that contain different numbers of animals these indices are unsuitable. In addition, both the Multiple Jaccard and Cody's measure, plus the Whittaker, Wilson and Shmida and Routledge measures are all affected by  $N$ , the number of time points sampled (test 11). As this study is also concerned with time series of differing lengths these indices can be discarded also. Routledge's measure also appears to be the least intuitive, taking a minimum of 0 and a maximum of 0.69.

There are therefore six indices that are worthy of further consideration for use in this study. Of these, it is clear from Table 4.3.1 that both the Dice and Jaccard measures (highlighted in blue) behave in a very similar manner. There is a difference in magnitude owing to the double weighting of  $a$  in the Dice index. Tulloss (1997) states that the Jaccard index is "undesirably depressed" and also that it is not linear. Nevertheless, these two indices behave intuitively and vary

similarly under the circumstances presented. Choosing between them may therefore be down to a matter of taste. One respect in which the Dice and Jaccard indices may be said to under perform is in their responses to tests 5 and 6. Here, both tests comprise the same number of animals in total to the standard data set but all animals that are not present at both time points are only present in the first (test 5) or last (test 6) time points. This is in comparison to animals that are not present at both time points being shared equally between time points. Clearly, these represent two quite different scenarios. However, the Dice and Jaccard indices return the same value for tests 5 and 6 as they do for the standard data set. For this reason Koleff et al. (2003) call the Dice and Jaccard indices "broad-sense" measures as they weight the shared component  $a$  too much at the expense of the gains and losses of individuals between samples. They advocate the use of "narrow-sense" measures which respond more to these changes in gains and losses. One such measure, and indeed the one which they advocate the most, is the Simpson index. It is clear from Table 4.3.1 that the Simpson index is indeed affected by tests 5 and 6, in both cases attaining the upper-most value of similarity. However, it is also clear from Table 4.3.1 that where the Simpson measure is beneficially affected by tests 5 and 6, it is not affected by tests 7 and 8. The Dice and Jaccard indices, on the other hand, are. Tests 7 and 8 are concerned with large scale efflux and influx of individuals. Whereas the Dice and Jaccard indices compute a value of similarity against this broader scale change, the Simpson measure is more restricted. It may again be down to taste as to which school of thought is the best for any situation. The reason for these differences is clear in that the Simpson index is designed to be unaffected by changes in  $S$  by calculating the proportion of the smallest sample that is shared

between samples (Magurran, 2003). Such behaviour seems undesirable because, firstly, when computing across a gradient in time the inconsistency of measuring similarity with reference to the smallest of two sample totals results in a value of diminished intuitive meaning. Secondly, in doing this much information is lost about changes in  $s$ , especially over prolonged time series.

The Social Cohesion index is akin to the Simpson measure in using the total of only one time point in the denominator and so is highlighted, along with the Simpson measure, in yellow. The difference between the two is that the Social Cohesion index always refers to the total at time 1 and so provides a consistent measure of the proportion of animals from time 1 that remain until time 2. Also, information is not lost about changes in  $s$  when computed over a time series as the result of a change in  $s$  is always quantified in the subsequent time step (other than that in the final time step). Koleff et al. (2003) refer to this as a measure of continuity and loss. They are put off the use of this measure by the fact that when  $a$  and  $b$  are small as a proportion of the additive total of  $a+b+c$ , the output is very sensitive to the value of  $b$ . This is, however, merely the effect of small numbers referred to above, brought to light by their use of proportional values for  $a$ ,  $b$  and  $c$ . The index of Social Cohesion seems to occupy a middle ground between the Simpson measure on one hand and the Dice and Jaccard measures on the other. Most importantly, tests 12 and 13 illustrate that when summarised over a time series the output is affected by all categories of change discussed. In test 12, 5 out of 15 individuals remain over one time step and 5 out of 5 at the next. The output of the Social Cohesion index is inflated by complete stability in the second time step and moderated by emigration in the first. Of course, the presence of the 10 new immigrants at the second time step

would not be quantified unless there was a subsequent time step. In this case the Simpson measure assumes the maximum value of similarity and the Dice and Jaccard measures are not responsive. In test 13 mass emigration is followed by mass immigration. In this example it is the Simpson measure that is unaffected, the Dice and Jaccard measures assuming much deflated values and the Social Cohesion index, again, taking a moderated, but less than standard, value. Over extended time series the Social Cohesion index therefore appears to be the most responsive, being higher than standard in test 12 due to the complete similarity evident in time step 1 and lower than standard in test 13 due to the small proportion remaining through time step 2. It is worth noting that on a grey seal breeding colony, immigration would be very low, if present at all, towards the end of the season.

Harrison's first and second measures (highlighted in green in Table 4.3.1) are the only examples of multiple sample indices to meet the basic requirements of this study. Interestingly, they produce quite different results, being frequently influenced in opposite directions by the test data sets. Harrison's second measure is most extreme in its behaviour and is akin to the reverse of the Simpson index in using only the largest value of  $s$  with which to measure change. As with Simpson's measure Harrison's second measure is intuitively unpleasing for the purposes of this study. Also, in using only the maximum value of  $s$ , all information is lost about changes in  $s$  (indeed, the reason for which this index was devised (Harrison et al., 1992)). Harrison's first measure behaves over two samples much like the Dice and Jaccard measures and is therefore subject to the same benefits and drawbacks. It also appears to behave well over multiple samples and does so in a similar fashion to the mean values of the Social

Cohesion index. Like the Social Cohesion index, Harrison's first measure is deflated to a lesser degree under test 12 and to a greater degree under test 13. Harrison's first measure is below standard under test 12 in comparison to the Social Cohesion index which is above standard, because Harrison's first measure is less inflated by the complete cohesion of animals across the second time step than is the Social Cohesion index.

The index to be used in this study must be robust over many different situations. One situation that is not covered by the previous tests is that of no animals being present at all. Table 4.3.2 illustrates such a situation. In test 14 animals are only present in 3 of 10 days and in test 15 animals are only present in 3 of 5 days. Over time steps when no animals are present it does not make sense to compute a value of social change as, if anything, this represents an asocial situation. That is, social change is neither at maximum nor minimum. For this reason change should only be estimated when animals are present. Harrison's first measure computes a value over the whole time series irrespective of the number of days in which animals are present. The measure of social cohesion, however, is only able to compute a value when an animal is present at the first of two time points and the Dice and Jaccard measures compute a value when there is an animal present at either the first or second of two time points. The results of this can be seen in Table 4.3.2. Test 14 consists of a longer time series than test 15. This could, for instance, represent the residence of two animals around whom it is desired to calculate change in the composition of neighbours. Animal 1 (test 14) is therefore resident for 10 time points and Animal 2 (test 15) for 5 time points. However, given the above it makes no sense to calculate change in the second half of Animal 1's residency as during that period it has no associates.

Table 4.3.2. Tests of social indices (14 and 15)

See text for details.

day	Test 14					Test 15				
	s	a	SSsc	SSd	SSj	s	a	SSsc	SSd	SSj
1	0	-	-	-	-	0	-	-	-	-
2	2	0	na	0	0	2	0	na	0	0
3	2	1	0.5	0.5	0.333	2	1	0.5	0.5	0.333
4	2	0	0	0	0	2	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0
6	0	0	na	na	na	-	-	-	-	-
7	0	0	na	na	na	-	-	-	-	-
8	0	0	na	na	na	-	-	-	-	-
9	0	0	na	na	na	-	-	-	-	-
10	0	0	na	na	na	-	-	-	-	-
mean SSsc			0.17					0.17		
mean SSd				0.13					0.13	
mean SSj					0.08					0.08
days	10					5				
S	5					5				
sum(s)	6					6				
mean(s)	0.6					1.2				
SSh1	0.81					0.79				
PTC			0.33	0.44	0.44			0.75	1	1

Harrison's first measure, however, does and this can be seen in the difference between index values from test 14 to test 15. If social change is not to be calculated in the absence of animals then these two values should be the same. The Social Cohesion, Dice and Jaccard values are the same over these two tests because they are incapable of computing change when no animals are present. Although the same values of social change are desirable it is clear that these two situations are far from identical. The value for test 14 is only representing the first half of the animals' residency, whereas the value for test 15 provides a more complete description of the social environment over the entire period of residency. It may therefore be necessary to calculate a secondary qualifier to describe the proportion of time over which a social index is computable. The Proportion of Time Computable (PTC) therefore explains the proportion of an animals residence for which a social index is able to describe social behaviour. Table 4.3.2 illustrates that under certain conditions the Dice and Jaccard indices are capable of 'describing' more than the Social Cohesion index.

#### 4.4 Post-hoc evaluation with real data

The above tests illustrate the different behavioural traits of each index and so their suitability to this study. Some appear better suited than others. The Dice, Jaccard and Social Cohesion indices appear most suitable and so worthy of further consideration. Although appropriate the tests described above are rather simplistic and it is worthwhile observing the behaviour of the short-listed indices when applied to real data. Elsewhere in this study simulations have been developed to provide a null model of behaviour against which to test the observed (see Chapters 5 and 6 for details). These simulations rely on observed site choice and movement to explain animal behaviour in the absence of any social ability. They are also, however, useful in providing a test-bed for these social indices. Here, indices can be subject to a large data set and so allowing a better understanding of their individual properties. Biologically realistic simulations illustrate the performance of indices in life-like scenarios. In the case of female grey seal breeding behaviour such simulations must include site choice and movement on the colony (see Chapter 5). However, this realism may also mask any undesirable properties inherent to the algorithm itself. Therefore it is also desirable to test the indices under more uniform conditions. To this end a set of simulations have been developed in which there were no constraints on site choice or movement. Social estimates were calculated within areas of the simulation arena as described fully in Chapter 5. Simulations and subsequent calculations were too extensive to be carried out by hand and so routines were written in R (R Development Core Team, 2004) (Appendix A.4.4-5).

There is an apparent trend under all three indices for output value to increase with denominator. Figure 4.4.1 illustrates this trend with a plot of mean

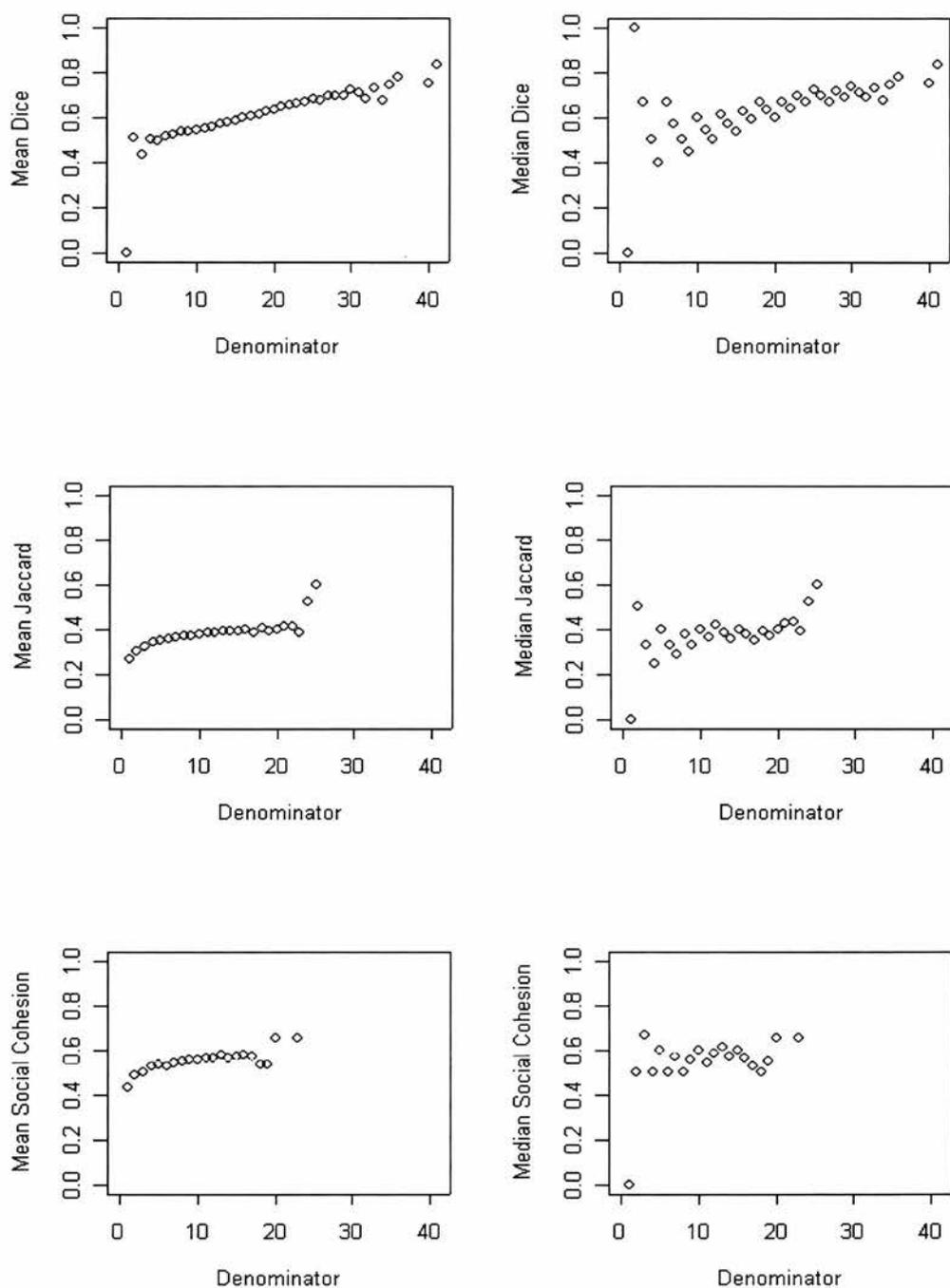


Figure 4.4.1. Social index values from 1000 simulations in which movement and site choice was restricted. Trends of mean and median index values of Dice (SSd), Jaccard (SSj) and Social Cohesion (SSsc) indices with the indices' denominator value.

and median index values for each denominator from all time-steps in 1000 simulations. This increase is most prominent in the Dice index but also noticeable in the Jaccard and Social Cohesion indices. All mean increases are statistically significant for linear regression ( $R^2 > 0.6$ ,  $p < 0.001$ ), even when trimmed for denominators with a count of less than 5 (i.e. those at the extreme tails of the distributions). All median increases are significant ( $R^2 > 0.19$ ,  $p < 0.05$ ) other than trimmed median Social Cohesion ( $R^2 = 0.14$ ,  $p = 0.13$ ). Covariance of output value with denominator in such a manner is undesirable as it may demonstrate a lack of standardisation. This endangers further analysis as values obtained at one denominator may not be comparable to those obtained at another. On the other hand this effect may be a real representation of animal behaviour within the simulation. As movement and site choice is restricted, animals may clump together more in certain areas, which therefore attain higher density than others. This may cause an increase in output with denominator, but may also mask further index properties.

Figure 4.4.2 illustrates mean and median index values for each denominator from all time-steps in 1000 simulations in which there was no restriction on site choice or movement. Lack of site choice has the effect of lowering denominator values as animals become less clumped and that combined with lack of movement restriction has the effect of lowering index values. The trend of increase with denominator is still obvious under the Dice index and this is significant ( $R^2 > 0.4$ ,  $p < 0.05$ ) apart from trimmed median Dice ( $R^2 = 0.23$ ,  $p = 0.11$ ). Increase in mean Jaccard values are not statistically significant ( $R^2 = 0.03$ ,  $p = 0.58$ ), unless trimmed ( $R^2 = 0.71$ ,  $p = 0.001$ ). This is highly significant, however the range of increase is minimal being 0.013 to 0.019. It is

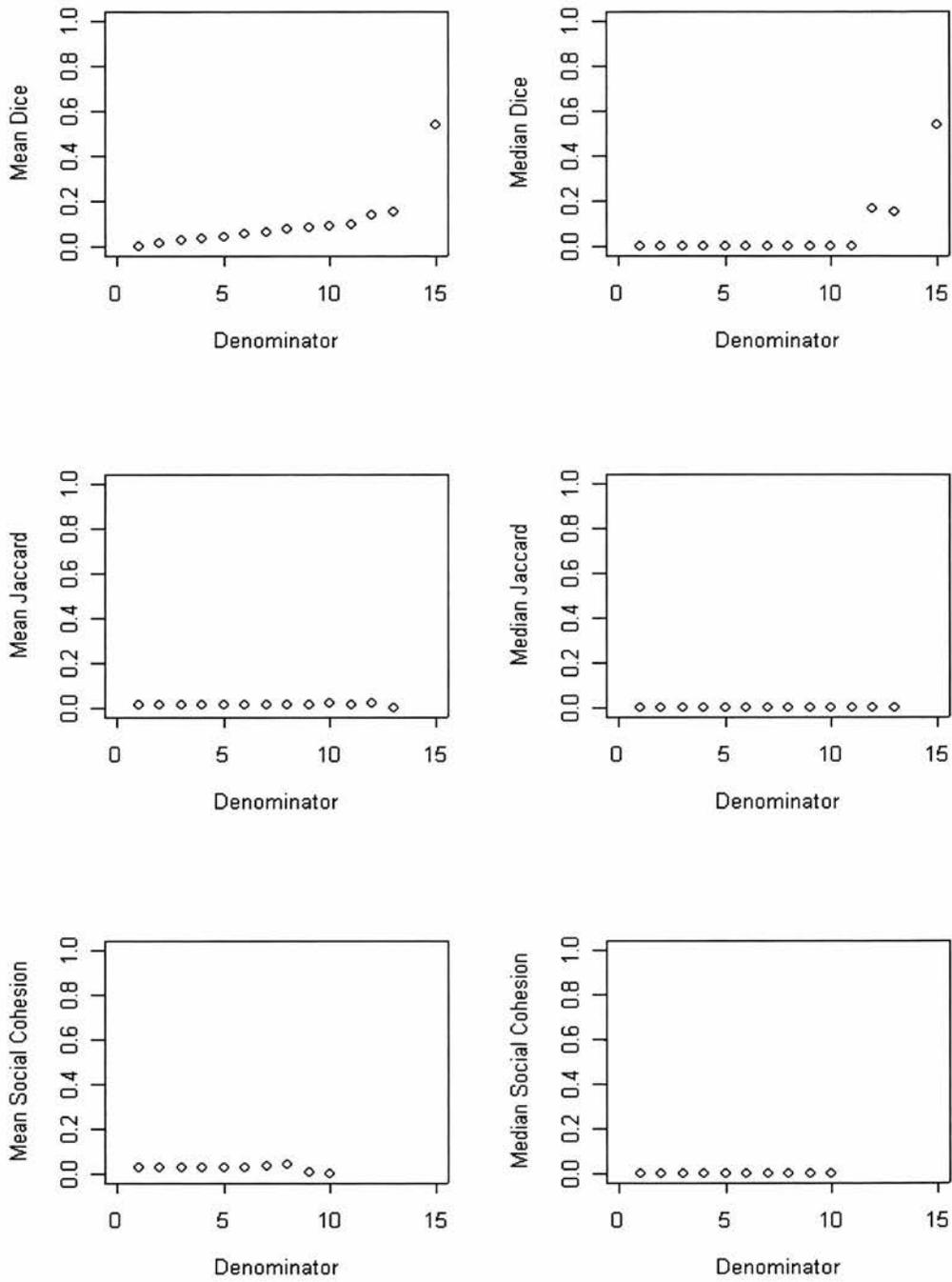


Figure 4.4.2. Social index values from 1000 simulations in which movement and site choice was not restricted. Trends of mean and median index values of Dice (SSd), Jaccard (SSj) and Social Cohesion (SSsc) indices with the indices' denominator value.

unlikely that this trend would mask any effect of real social behaviour. There is no significant trend in mean Social Cohesion values ( $R^2 < 0.2$ ,  $p > 0.05$ ) although these show a similar, almost negligible, increase to the Jaccard values. All median Jaccard and Social Cohesion values are 0. This demonstrates that under the Dice index at least, there is still an observable increase in output value with denominator irrespective of restriction to site choice and movement. Further explanation is needed. Both simulations, although based on a real and technically open population, involve an effectively closed population. This is because the number of animals in the simulation arena is limited. Therefore, if by chance a certain number of animals are present in one area at one time point, these constitute a certain proportion of the closed population. Even within the free mixing of the second simulation, if this number of animals is increased, the likelihood of any animals re-occurring in that same area at the next time point is also increased and so the resultant output value will be increased. These effects appear most exaggerated under the Dice index. Although under real life conditions the Dice index is accurate in describing the social environment, it would be desirable for this effect to be minimised. As such the Jaccard and Social Cohesion indices seem most suitable in being least affected by denominator.

#### 4.5 Discussion

No single measure for quantification of change in the social environment has been found that incorporates all aspects that would be beneficial to this study. None the less, two measures have been pinpointed that satisfy the two main requirements in being invariant to  $S$ , the number of animals concerned, and  $N$ , the number of time steps in a series. The Jaccard and Social Cohesion measures are only let down by being pair-wise measures and so unable to produce a single value over an extended time series. This, of course, can be overcome with the use of a summary statistic such as the mean or median. These two measures have slightly different emphasis. Social Cohesion quantifies just that, the maintenance of association between animals from one time point to the next. In this context the Jaccard coefficient appears to be a more definitive measure of social stability, in quantifying a compound value for both maintenance of old associations and establishment of new ones.

Initially the Dice and Jaccard indices appear very similar, but when subject to an extended data set of the type to be encountered in this study it appears that the Dice output is excessively affected by denominator. Although this is due to animal behaviour and so a real description of the environment is produced, this effect is best minimised if samples of varying denominator are to be compared. As such the Jaccard index is most suitable. The Jaccard index was unresponsive to social change in tests 5 and 6 but this is more intuitive when thought of in terms of social stability. Although tests 5 and 6 represent different situations to each other and the standard data set in detail, they are clearly similar in terms of overall change as a proportion of unique individuals. This property must be inherent to any interpretation of Jaccard outputs. This represents a form

of aliasing (Tulloss, 1997). However, this loss of detail, or aliasing, to a certain extent is what is aimed for when summarising data with the use of an index. Linearity can be defined as the constancy of incremental changes in output value when input value is changed by one unit (Tulloss, 1997). When all else is constant, the Jaccard index is linear. Being a simple proportion, the Social Cohesion index is linear also. The Social Cohesion index can be thought of as more specific than the social stability estimate provided by the Jaccard index and as such may explain a smaller proportion of behaviour. The Jaccard index is therefore supported for use in this study.

Turnover of individuals within an assemblage has rarely been quantified at the level of detail attempted here. Summers et al. (1985) quantified replacement of geese using a feeding ground but no attempt was made to identify individuals. The method of social stability presented here may also have utility for other studies. For instance, although social stability may be inferred from representations of social structure based on the strength of individual associations, it is not known directly. An assessment of change within groups of animals, for instance cetacean pods, may be useful to complement traditional measures and add further insight to the social structure of such systems.

Of course, even after a suitable index has been found the scale over which to compute it requires careful consideration. In this study spatial association is defined as presence within a certain distance (Whitehead & Dufault, 1999). Variation in this distance will obviously alter the inference that can be made. For instance, a small distance may allow inference at the scale of individuals whereas a large distance may allow inference on the scale of groups. Similarly any index can be computed over a variety of time scales, either on day to day behaviour

within a season or year to year behaviour over an animals life. Investigation of index values over varying time scales may also be instructive (Russell et al., 1995). For instance, over what time scale do animals start to be replaced and over what time scale are all animals replaced?

Even if variation in the social environment is found, this does not provide any information as to causation. That is, social structure may be a passive by-product of some other feature of the environment, such as seals' preference for a certain type of topography. It is therefore desirable to test the observed index values for randomness. Non-random values would suggest an active mechanism for the promotion of social behaviour. Monte Carlo methods of randomisation have been widely advocated as a powerful tool for detecting non-randomness of social test statistics (Adams & Anthony, 1996; Bejder et al., 1998; Whitehead, 1999; Whitehead & Dufault, 1999). Here, the observed data may be permuted under certain constraints to produce a distribution of sample statistics (Jaccard values). Hypothesis testing is then carried out by comparing the observed test statistic to the distribution of simulated test statistics. If the observed value falls outwith the confidence intervals of the simulated values then the null-hypothesis of randomness can be rejected. Although such a finding would be persuasive of the importance of social structure, it is not a requirement for further investigation. Even if variation in social structure is a passive by-product of some other process, that variation may have further consequences to other aspects of an animal's life.

# **Chapter 5**

## **Within year sociality**

5.1 Introduction

Grey seal mothers breeding on North Rona, Scotland, have the opportunity to both choose and influence the social environment in which they raise their pups. On this colony the primary breeding areas are located inland where access to the sea is restricted. As such breeding females do not generally return to the sea during lactation, but stay close to their initial pupping sites (Anderson et al., 1975, Chapter 2). The most common form of interaction between breeding grey seal mothers is agonistic and most commonly initiated in close proximity (Anderson & Harwood, 1985; Boness et al., 1982). In other colonies, such as that on the Isle of May, Scotland, mothers do commute between sea and pup during lactation and the resultant jostling of positions results in higher rates of interaction (Redman, 2002). Even within the Isle of May colony there are areas of higher quality than others in which females are able to spend more time interacting with their pup and less time in locomotion (Twiss et al., 2000). The more sedentary behaviour of North Rona mothers therefore provides a less antagonistic environment in which to raise a pup. In addition, a less fluid social organisation provides the opportunity for familiarity to grow between adjacent individuals. (Of course, familiarity may also be influenced by historic relationships. Such longer-term social processes that may operate across breeding seasons are investigated in Chapter 6.) Familiarity is often associated with a reduction in aggression (for instance: Johnsson, 1997; Utne-Palm & Hart, 2000), further enhancing the possibility of reduced antagonism in areas of elevated social stability. A grey seal mother gives birth to one pup per season and feeds it for up to three weeks before weaning. The most common causes of death in pre-weaned pups stem from disruption of the mother-pup bond (Anderson et al.,

1979) and the larger a pup is at weaning, the higher are its chances of survival in the first year of life (Hall et al., 2001). The more stable and less aggressive the environment that a pup is reared in then, the higher it would seem are its chances of successful feeding and survival.

The breeding arena itself consists of variable topographical features and females preferentially locate where there is good access to water (Anderson et al., 1975; Twiss et al., 2001). This may be to aid in thermoregulation or maintenance of water balance while fasting (Twiss et al., 2002). On North Rona the subsequent distribution of females reaches inland to cover most areas where access to pools of fresh water is good and the slope and elevation of the terrain is not too extreme. Maternal success can also be highly variable, as measured by both efficiency of lactation and contribution to the colony-wide genetic pool (Pomeroy et al., 1999; Pomeroy et al., 2001). In addition the most successful mothers tend to inhabit the highest quality areas. These areas are also those that may be expected to contain a more stable social environment, being away from thoroughfares leading to the sea and in areas with good access to preferred resources. In these areas the need for movement and associated antagonism is therefore reduced.

In this chapter, social stability is first quantified across the North Rona breeding colony. Social stability is calculated using both area and individual based approaches (Section 5.2). The suitability and success of the social stability calculations are then assessed by analysing sensitivity of the method to spatial grain, completeness of the data source and temporal inconsistency of the sampling regime (Section 5.3). Observed values of social stability are also tested for significant deviation from a null model based on site choice, within season

movements and temporal attendance patterns (Section 5.4). These are the three main factors that may influence social stability if it were a passive artefact of non-social behaviour. Evidence of the contrary, however, would suggest active behavioural organisation of sociality within the colony. The influence of topographic quality, aggressive behaviour and reproductive synchrony on observed social stability is investigated in Section 5.5. Finally, the subsequent influence that social stability may have on reproductive success is investigated in Section 5.6.

## 5.2 Quantification of sociality for areas and individuals

### 5.2.1 Methods

Social stability within the study area on North Rona was quantified within the 2002 and 2003 breeding seasons using the Jaccard (SSj) index as described in Chapter 4. The survey dates and identification data for both years are shown in Table 2.3.1.1 (Chapter 2). SSj is computed by dividing the number of identities common to two (successive) surveys by the total number of identities present over those surveys and therefore provides a measure of social change between surveys. This was implemented both within areas to provide a spatial map of sociality, and around individuals to quantify the social stability that each animal in the study area experiences.

#### Area-based social stability (A-SSj)

In Chapter 3 it was estimated that the spatial scale of association for animals in the study area is 10m. This is because animals that are separated by 10m or less are potential interactants, and so may have behavioural influence on one another. Calculation of social stability is therefore carried out at a scale of 10m to provide a measure that is meaningful in comparison to what an individual experiences.

This spatial scale was implemented by overlaying the study area with a grid of 10m by 10m cell size (see Figure 2.1.2, Chapter 2). Social stability could be calculated on the identities within the limits of each grid cell. A benefit of this approach would be that the area represented by each grid cell is unique. A disadvantage, however, is that the inclusion/exclusion of an individual to a particular cell would be excessively arbitrary at the grid intersections due to edge

effects. For instance, two individuals that are only 1m apart may be allocated to two different cells. However, it would seem likely that they may have more influence on each other than with other individuals at opposite extremes of the cells to which they were allocated. As the focus here is to evaluate the social stability that individuals would actually experience this method was discounted.

A more meaningful method is to calculate social stability at a 10m radius around each grid cell centre. This provides a measure of the social stability that an individual would experience if it was located at the centre of a grid cell. Spacing these centres at 10m intervals gives a reasonably continuous measure of social stability across the study area (maximum dimension 100m). A disadvantage to this method is that neighbouring circular areas will necessarily overlap. The result of this is a lack of independence between neighbouring areas. However, it is quite realistic to assume that two animals, although outwith the spatial range of influence to each other may share and be influenced by common neighbours. This non-independence then is, although statistically undesirable, biologically realistic. Studies concerned with pair-wise indices of association will also be susceptible to such non-independence as individuals may have multiple associations (see for instance: Chilvers & Corkeron, 2002; Underwood, 1981; Whitehead et al., 1991). A lack of independence between neighbouring areas is common in spatially structured data, and known generally as spatial autocorrelation (Sokal & Oden, 1978). The statistical treatment of spatial autocorrelation is discussed below, and further in Section 5.6 of this chapter. Area-based social stability (A-SS<sub>j</sub>) values were calculated by implementing the SS<sub>j</sub> algorithm on the identities present within a 10m radius of each of the 10m grid cell centres shown in Figure 2.1.2. A summary of A-SS<sub>j</sub> values over the

entire season is provided by the median. This summary statistic was chosen as it provides a robust central tendency to data when skewed (for instance if there are many zero A-SSj values) and approximates to the mean when normal. A-SSj values were calculated using the "socarea" function (see Appendix A.1), written by the author for this study in R (R Development Core Team, 2004).

#### Individual-based social stability (I-SSj)

It is also desirable to quantify the social stability that each individual actually experiences. Seals are mobile and may move between areas or reside mid-way between grid cell centres. In addition, the average length of stay for a mother on the North Rona colony is approximately three weeks (Pomeroy et al., 1999). In both years of study surveys were carried out over approximately six weeks and so the temporal extent over which area and individual based social stability values were calculated are different. For these reasons, even if a seal is predominantly located within one area, the method above may not best describe the social stability that it experiences. Individual-based social stability (I-SSj) was therefore calculated by implementing the SSj algorithm on the identities within 10m of each individual during its residence on the colony. Like A-SSj values, I-SSj can be summarised over an animal's stay with the median and may suffer from non-independence if calculated around individuals that are less than 20m apart. I-SSj values were calculated using the "socind" function (see Appendix A.2), written by the author for this study in R (R Development Core Team, 2004).

Proportion of Time Computable using SSj (SSj-PTC)

SSj values are only computable when animals are present within the 10m search radius. An SSj value of zero describes no stability when no individuals are common to two surveys. When no animals are present at all, however, there is no sociality to be measured and so an SSj value is not available (NA). If the number of surveys during which animals are present in different areas is not the same, then the median value of SSj will describe social stability over different timescales. For instance, animals may only be present for five days over the whole season in area A, but present always in area B. Sociality can, therefore, only be computed by the A-SSj algorithm for a proportion of the time in area A, but for the full time in area B. This is equally applicable to I-SSj calculations. A measure of the proportion of time that SSj is computable (SSj-PTC) is therefore provided to illustrate the temporal extent that is represented by each median SSj value. This was calculated by dividing the number of survey intervals over which SSj was actually computed by the number of survey intervals over which it would be theoretically possible to calculate SSj, should animals be present.

Statistical analysis

Statistical analysis was carried out to assess differences in within year SSj values between the two years under study. As stated above, spatial structure in the data may lead to the statistical problem of spatial autocorrelation. This is where values at one area are more or less similar to those at neighbouring areas than would be expected by chance (Sokal & Oden, 1978). To address this issue, Mantel tests were used to examine spatial autocorrelation within the data and partial Mantel tests were used to control for it in subsequent correlation analysis.

Testing for correlation between A-SSj values will assess whether areas are of similarly high or low A-SSj in both years. Mantel tests are computed on distance, or dissimilarity, matrices. Such a matrix describes the difference between values of (or Euclidian distance between) samples. The Mantel test assesses linear correlation between two distance matrices. Here the Mantel test is used to assess correlation between A-SSj values and Euclidean distance. A significant correlation suggests spatial autocorrelation is present in the data. The partial Mantel test assesses correlation between two distance matrices while controlling for correlation with a third. Partial Mantel tests are used here to assess correlation between within year A-SSj from the two years of study while controlling for Euclidean distance and so spatial autocorrelation. Significance is tested by permutation (see Legendre, 2000). Mantel and partial Mantel tests were carried out using PASSAGE (Rosenberg, 2004b). Mantel tests could not be carried out on I-SSj values between years as individuals did not occupy the same locations in both years and so spatial structure was not constant.

Paired-sample Wilcoxon signed-ranks tests were used to investigate any general shift in the distribution of within year SSj to higher or lower values in consecutive years. A paired sample test was necessary to compare the values for areas and individuals that were present in both years. Wilcoxon tests were carried out in SPSS 11.0 (SPSS\_Inc.). It was not possible to control for spatial autocorrelation in this test.

### 5.2.2 Results

#### Area-based social stability (A-SSj)

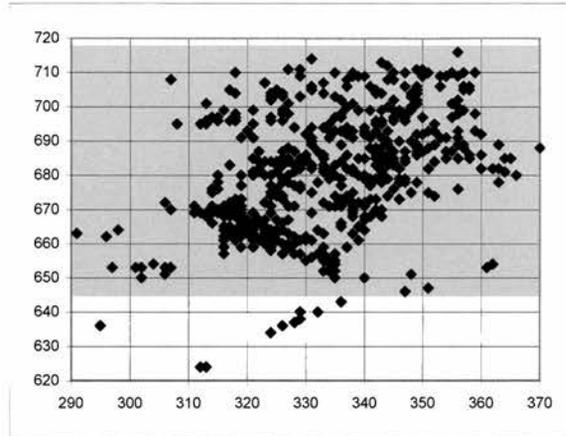
Median A-SSj values were available for 57 grid cell centres in 2002 and 54 grid cell centres in 2003. Therefore although the study area and number of animals observed increased from 2002 to 2003 (see Chapter 2.1), the proportion of this area actually used by the seals (and so having an associated A-SSj value) decreased. This is due to a few outlying animals using the periphery of the colony in 2002, as can be seen in Figure 5.2.2.1.

There was considerable variation in median A-SSj values across the study area in both years (Figure 5.2.2.2(a)+(b)). In 2002 median A-SSj values ranged from 0 to 0.67 with a median of 0.17, and in 2003 median A-SSj values ranged from 0 to 1 with a median of 0.33.

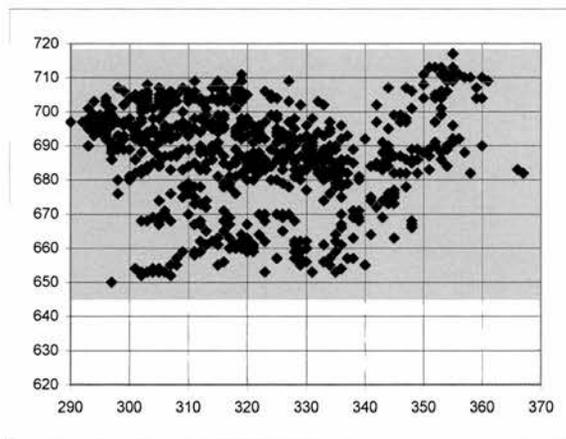
The variability in A-SSj values throughout each season appears greater in peripheral areas, as illustrated by interquartile range values (Figure 5.2.2.2(c)). Sociality also appears to be computable over a smaller proportion of time in these areas (Figure 5.2.2.2(d)). As an example to aid interpretation of this, it appears that area (350,660) in 2003 has a high value of social stability (A-SSj = 1.00). However, the variation in A-SSj here appears to be large also (A-SSj interquartile range = 1.00). In addition, this value of A-SSj is only computable over 25% of the season's duration, the remaining 75% of the season in that area not being associated with any animal presence (A-SSj-PTC = 0.25). This area is therefore not of consistently high social stability as may have been inferred from Figure 5.2.2.2(b) alone.

There were 45 locations for which within year A-SSj values were available in both 2002 and 2003. There was no general difference in the

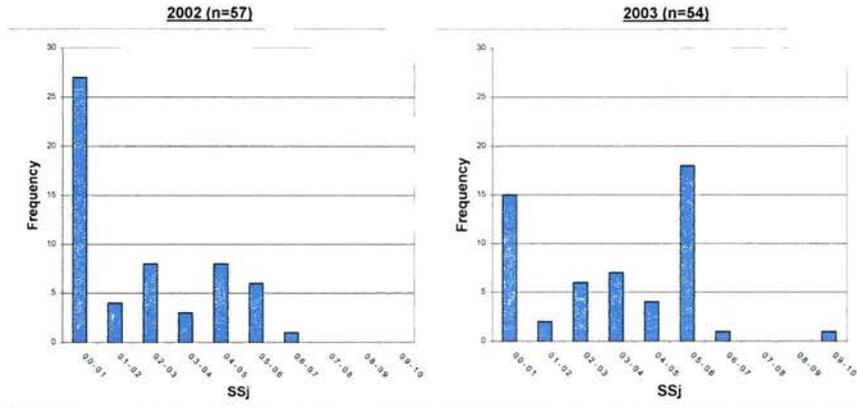
**2002**



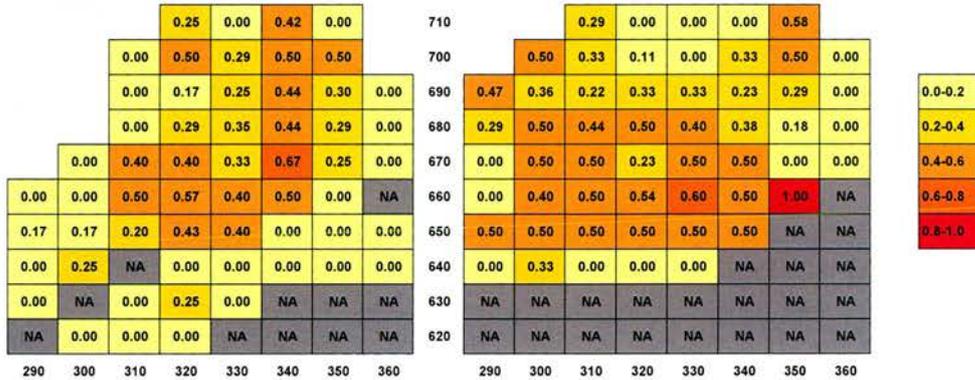
**2003**



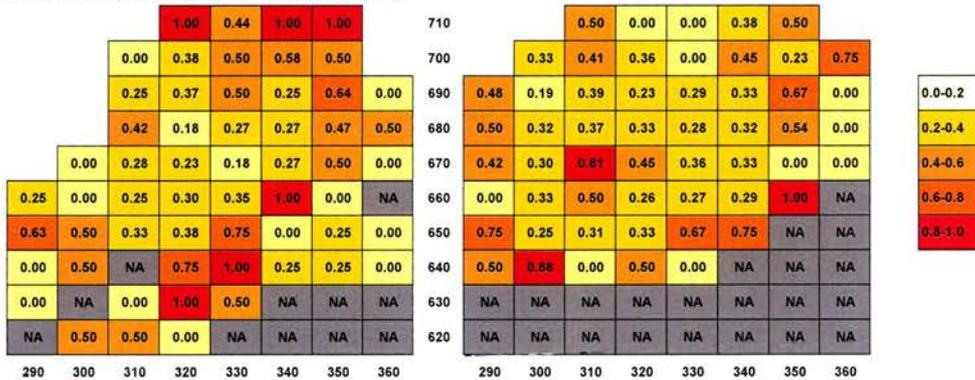
**Figure 5.2.2.1.** Geographical distribution of all seal locations in 2002 and 2003. Axes represents OSGB eastings (prefix 181\*\*\*) and northings (prefix 1032\*\*\*). Map units are in metres.



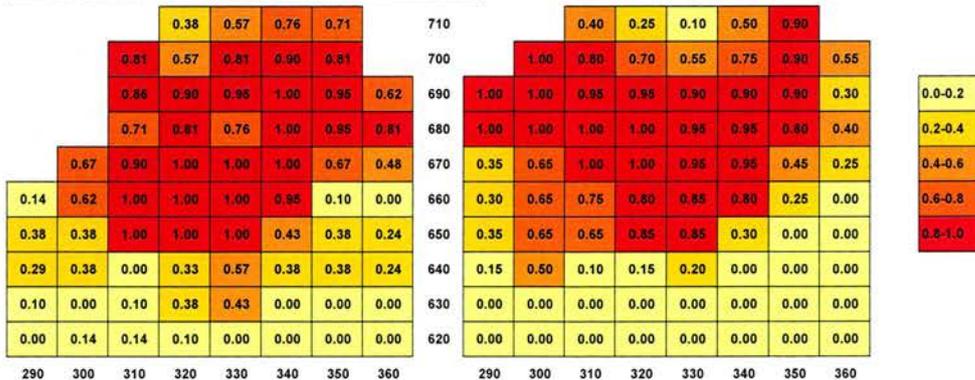
a) Frequency distributions of median A-SSj values



b) Geographical distributions of median A-SSj values



c) Geographical distributions of A-SSj interquartile range values



d) Geographical distributions of A-SSj-PTC values

Figure 5.2.2.2. Distributions of median A-SSj, A-SSj interquartile range and A-SSj-PTC values in 2002 and 2003.

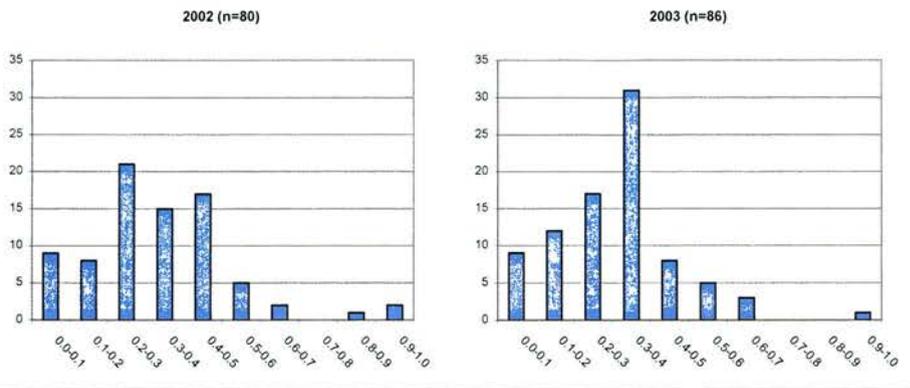
Each value is calculated at a 10m radius around each grid cell centre

(b)-(d) Axes represents OSGB eastings (prefix 181\*\*\*) and northings (prefix 1032\*\*\*). Map units are in metres.

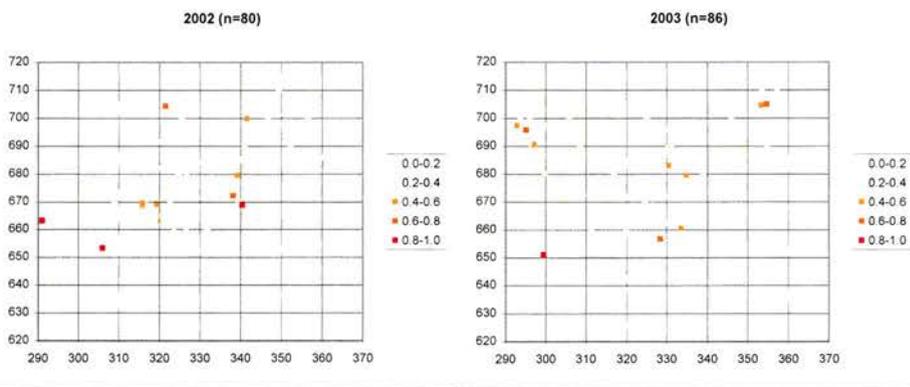
frequency distributions of within year A-SSj values between years in these locations (Wilcoxon:  $n=45$ ,  $Z=-1.77$ ,  $p>0.05$ ). However, there was a difference in the geographical distribution of values. Mantel tests showed spatial autocorrelation was present in the A-SSj values in 2003 (Mantel:  $n=45$ ,  $Mcoef=0.1417$ ,  $p<0.05$ ) but not in 2002 (Mantel:  $n=45$ ,  $Mcoef=-0.0027$ ,  $p>0.05$ ). Any correlation between 2002 and 2003 A-SSj values was not significantly different to chance when spatial structure was taken into account (Partial Mantel:  $n=45$ ,  $Mcoef=0.0605$ ,  $p>0.05$ ). So, there was no general increase or decrease in within year A-SSj values between years, but the geographical patterning of values was different.

#### Individual-based social stability (I-SSj)

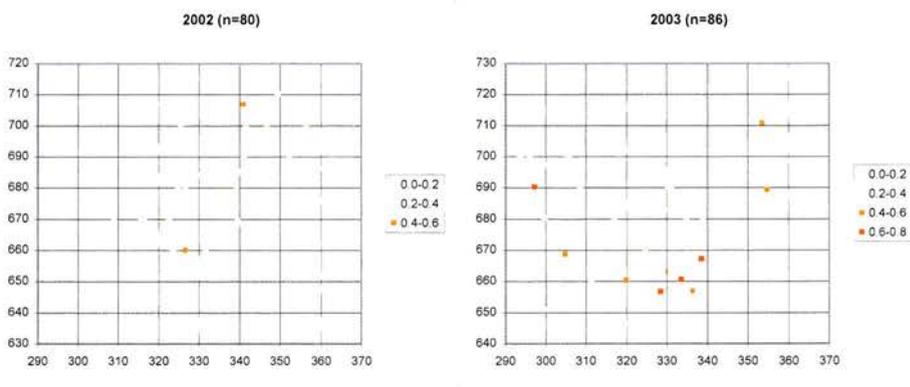
There was considerable variation in the social stability experienced by individuals within the study area in both years (Figure 5.2.2.3(a)+(b)). Of the 105 individuals in 2002 and 118 in 2003, median I-SSj values were available for only 80 and 86 individuals in those years respectively. This is because the proportion of time for which I-SSj was computable was zero for individuals whose presence was ephemeral in the study area. That is, I-SSj values were not computable for animals which were not observed in consecutive surveys or were only observed once. It is important to note that individuals were not static throughout the season and so the spatial representation of I-SSj values in Figure 5.2.2.3(b)-(c) are based on seasonal centroid locations. I-SSj ranged between 0 and 1 with medians of 0.31 in both 2002 and 2003. As with A-SSj values, I-SSj appears more variable towards the periphery of the colony (Figure 5.2.2.3(c)). I-SSj was computable for a high proportion of individuals' stay in most cases (Figure



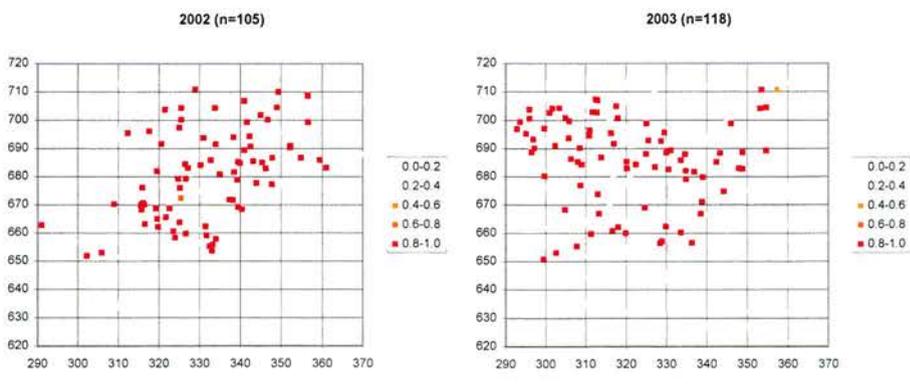
(a) Frequency distributions of median seasonal individual-based SSI values



(b) Geographical distributions of median I-SSi values



(c) Geographical distributions of I-SSi interquartile range values



(d) Geographical distributions of I-SSi-PTC values

Figure 5.2.2.3. Distributions of median I-SSi, I-SSi interquartile range and I-SSi-PTC values in 2002 and 2003. (b)-(d) Axes represents OSGB eastings (prefix 181\*\*\*) and northings (prefix 1032\*\*\*). Map units are in metres.

5.2.2.3(d)). Non-zero I-SSj-PTC was more than 0.75 in 78 out of 80 cases in 2002 and 82 out of 86 cases in 2003. This is because most individuals had another female within 10m most of the time.

There was no difference between the distribution of within year I-SSj values in 2002 and 2003. There were 38 individuals present in both years and a Wilcoxon test showed no general increase or decrease in I-SSj values for these (Wilcoxon:  $n=38$ ,  $Z=-.69$ ,  $p>0.05$ ).

### 5.2.3 Discussion

This study has demonstrated a variance in social stability across the grey seal breeding colony on North Rona, Scotland. In general, areas towards the periphery of main aggregations tend to have a less constant pattern of seal residence than those towards the centre. However, even in well used areas there appears to be variation in A-SSj with evidence of hot spots surrounded by moderate values. There was no general quantitative shift in A-SSj values between years. However, neither were they constant. A change in the area used by seals in 2003 saw the main aggregation spreading to an area that was not used much in 2002, and with it an increase in social stability. This change in the spatial pattern of social stability explains the lack of spatial correlation in A-SSj values between years. The variation in A-SSj is reflected in the distribution of I-SSj values experienced by each individual, some mothers having higher social stability than others.

Breeding aggregations on North Rona tend to be focussed around access to resources such as pools of water (Anderson et al., 1975; Twiss et al., 2000). It might seem intuitive then, that social stability would be reduced towards the

centre of aggregations as animals would interchange here more often to gain access to those resources. However, this appears not to be the case, as social stability is consistently higher towards the centre of aggregations. Animals towards the periphery of the colony must therefore move around more, perhaps to access more limited resources or through greater levels of disturbance. However, the quantification of social stability is about more than just movement. Although instability may be created by movement it is the coordination of such movement either within an area or between individuals and resultant dynamics of association that the measure of social stability encapsulates. What the results show us then, is that some animals in some areas are more socially cohesive and less affected by influx and efflux of individuals than others. What drives this (a side effect of resource availability or active social behaviour?) is addressed in subsequent sections of this chapter.

Redman (2002) (and subsequently Pomeroy et al. 2005, see Chapter 6) described between year pair-wise associations on this colony but until now nothing was known about the social environment within a single breeding season. Although long term associations have definite implications for the arguments presented here (familiarity leading to aggression reduction, for example: Johnsson, 1997; Utne-Palm & Hart, 2000), it is clear that the short term environment that an animal experiences may have a profound influence on its own behaviour and so possibilities for, in this case, reproductive success. Providing a within year measure of the social environment allows us to add social processes to the list of environmental variables available for investigating what factors may influence a grey seal mother in her choice of pupping site and subsequent success in raising her pup.

### 5.3 Sensitivity Analysis

#### 5.3.1 Methods

The results produced here are dependent upon a number of assumptions. In the context of this study it is important to understand how variation in structure and completeness of the raw data and scale parameters in the quantification process can affect output. The following investigation was carried out on data from 2003 only.

#### Missing data

Missing data in this study stems from the presence of unidentified animals within the study area. Reclassification of these animals by assigning theoretical identities allows the investigation of how sensitive the output is to these data points. Unidentified animals can be reclassified to one of two states, as a new and previously unseen identity, or as an already known identity. The most conservative test may be to allocate new identities to all unidentified animals, however this may also be the most unrealistic. It is most likely, given observed animal behaviour, that unidentified animals are actually animals of known identity from nearby in time and space. Therefore, two test data sets were constructed; 1. 'As New' in which all unidentified animals were assigned a new identity; and 2. 'Reassignment' in which unidentified animals were assigned an identity from those within a certain radius of the missing data point, either one survey before or after but not during the survey in question. Where this was not possible, an identity was reclassified as new. This procedure was carried out using the "unidentifieds" function (see Appendix A.3), written by the author for

this study in R (R Development Core Team, 2004). These were compared to the 'Standard' data set described in the previous section of this chapter.

#### Spatial effects : Scale

The most influential parameter within the quantification process is that of scale. In this study behavioural evidence suggests a suitable scale of 10m, but here the implications of using a different spatial grain are investigated. Social stability was therefore recalculated at 5m and 20m scales.

#### Spatial effects: Grid placement

The output may also be sensitive to the exact location of grid cell centres around which social stability is quantified. The grid was therefore shifted 5m to the right and social values recalculated.

#### Temporal effects: Inter-survey interval

Temporal structure of the raw data may also affect output. For instance, the time interval between surveys may affect the resultant social stability values if animals are more or less likely to have moved given increasing or decreasing intervals. Output values were investigated with respect to the interval over which they were calculated.

### 5.3.2 Results

#### Missing data

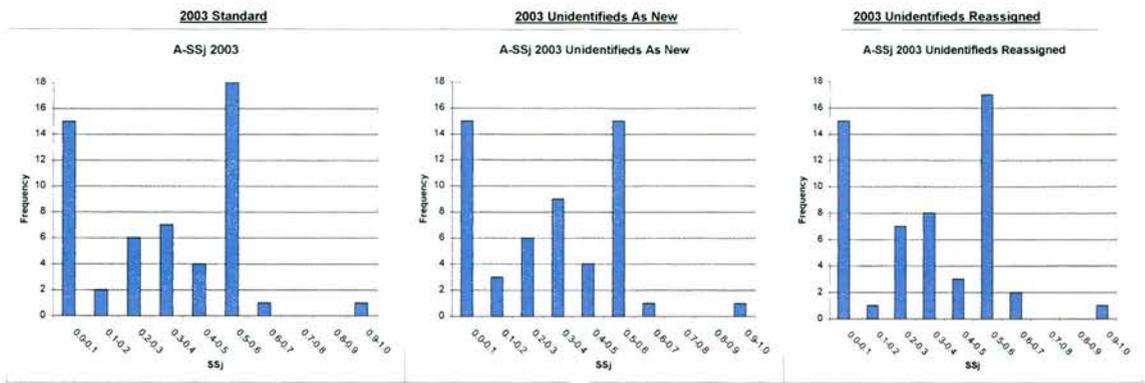
Reclassifying all 55 unidentified animals from 2003 as new produced a total of 173 individuals. Using a 10m search radius resulted in reassignment for

93% of unidentified animals and complete reassignment was available at a scale of 20m (Table 5.3.2.1). Although it is possible that animals moved further than 10m, this seems unlikely in most cases and complete reassignment is not necessarily the most realistic scenario. Only reassignment at 10m was considered further.

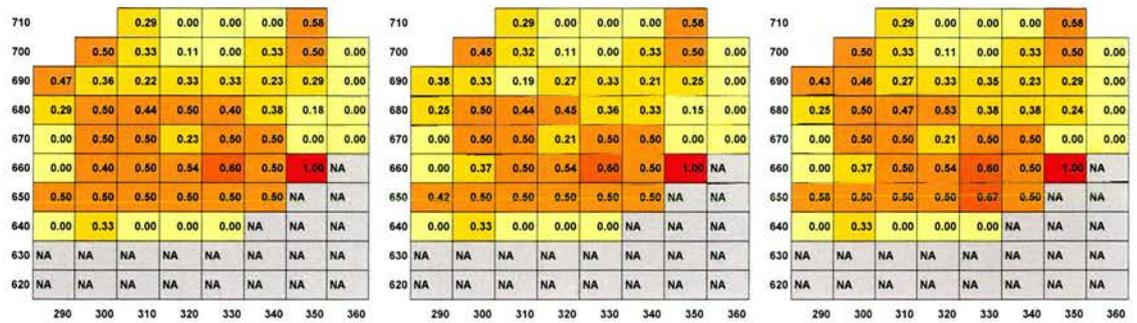
Table 5.3.2.1 Results of As New and Reassignment conditions. Total: the total number of identities resulting from each condition. Reassigned: denotes the total number of identities for which a reassignment identity was available. As New: the number of identities reclassified as new.

	As New	Reassignment at 10m	Reassignment at 20m
Total	173	122	118
Reassigned	-	51	55
As New	55	4	0

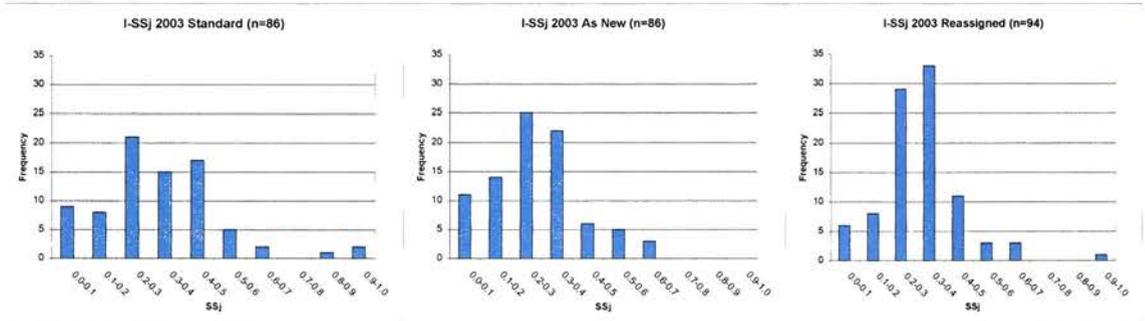
Figure 5.3.2.1 shows the distribution of A-SSj and I-SSj values from the Standard, As New and Reassigned data sets. Table 5.3.2.2 shows the quartile SSj values produced in each case. There is no difference in the spatial patterning of A-SSj values in As New or Reassigned data sets when compared to Standard. As New and Reassignment outputs are highly correlated with Standard even when spatial structure is taken into account (Partial Mantel: Standard-As New:  $n=54$ ,  $M_{\text{coeff}}=0.9883$ ,  $p<0.05$ ; Standard-Reassignment:  $n=54$ ,  $M_{\text{coeff}}=0.9774$ ,  $p<0.05$ ). However, paired-sample Wilcoxon tests suggest that the As New output contains a general shift to lower A-SSj values (Wilcoxon:  $n=54$ ,  $Z=-3.743$ ,  $p<0.05$ ). No such effect was observed in the Reassignment output (Wilcoxon:  $n=54$ ,  $Z=-1.058$ ,  $p>0.05$ ).



(a) Frequency distributions of median A-SSj values



(b) Geographical distributions of median A-SSj values



(c) Frequency distributions of median I-SSj values

Figure 5.3.2.1. Distributions of median A-SSj and median I-SSj under Standard, As New and Reassignment conditions

(b) Axes represents OSGB eastings (prefix 181\*\*\*), and northings (prefix 1032\*\*\*). Map units are in metres.

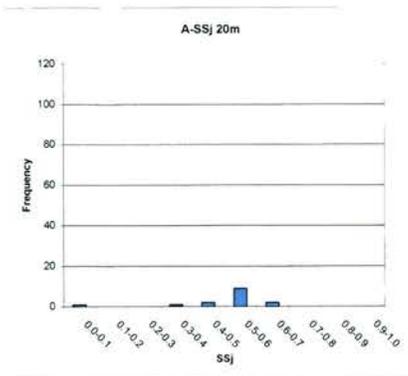
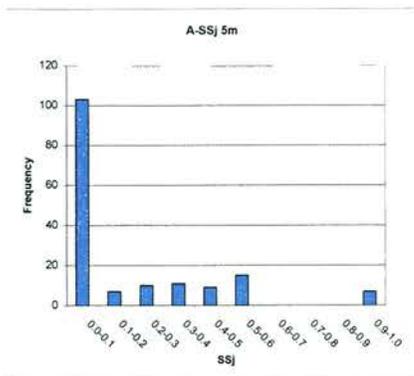
I-SSj vales are also highly correlated (Partial Mantel. Sandard-As New: n=83, Mcoeff=0.8656, p<0.05; Standard-Reassignment: n=83, Mcoeff=0.6153, p<0.05). However, the As New data set appears to include a general shift to lower I-SSj values (Wilcoxon: n=83, Z=-6.806, p<0.05) while the Reassignment data set includes a general shift to higher I-SSj values (Wilcoxon: n=83, Z=-2.481, p<0.05). In Table 5.3.2.2, an apparent reduction in I-SSj-PTC quartile values in the Reassignment data set stems from an increase in the number of ephemeral 'as new' animals for which an I-SSj-PTC value of zero is assigned.

Table 5.3.2.2 A-SSj and I-SSj quartile values from missing data, spatial effects and temporal effects conditions

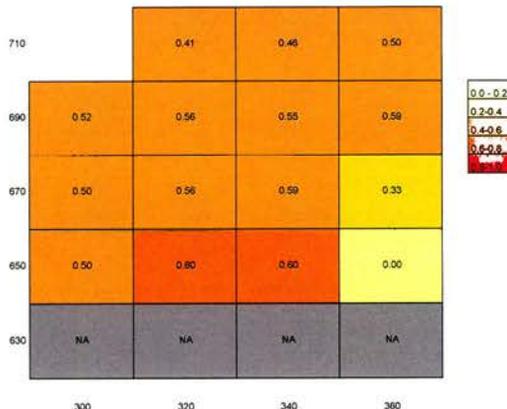
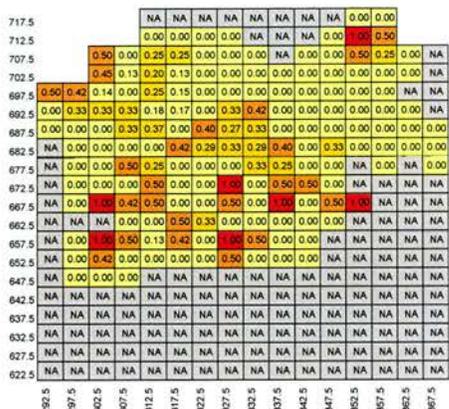
Condition		Q1	Q2	Q3		Q1	Q2	Q3
Standard	A-SSj	0.00	0.33	0.50	I-SSj	0.20	0.31	0.37
	PTC	0.00	0.48	0.90	PTC	0.00	1.00	1.00
As New	A-SSj	0.00	0.33	0.50	I-SSj	0.18	0.27	0.34
	PTC	0.00	0.48	0.90	PTC	0.00	0.00	1.00
Reassignment	A-SSj	0.00	0.34	0.50	I-SSj	0.24	0.31	0.37
	PTC	0.00	0.48	0.90	PTC	0.50	1.00	1.00
5m Scale	A-SSj	0.00	0.00	0.33	I-SSj	0.00	0.04	0.19
	PTC	0.00	0.10	0.55	PTC	0.00	0.71	1.00
20m Scale	A-SSj	0.48	0.52	0.57	I-SSj	0.41	0.46	0.52
	PTC	0.45	0.90	1.00	PTC	0.00	1.00	1.00
5m Shift	A-SSj	0.00	0.33	0.49				
	PTC	0.00	0.50	0.90				

Spatial effects: Scale

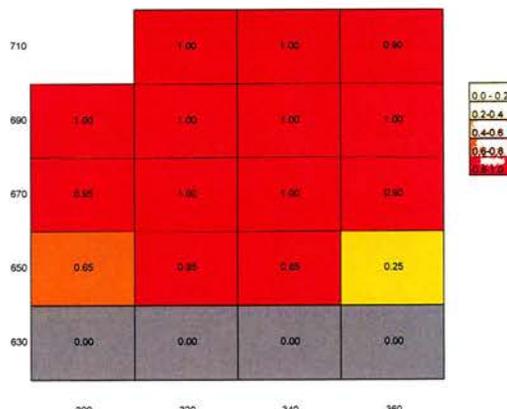
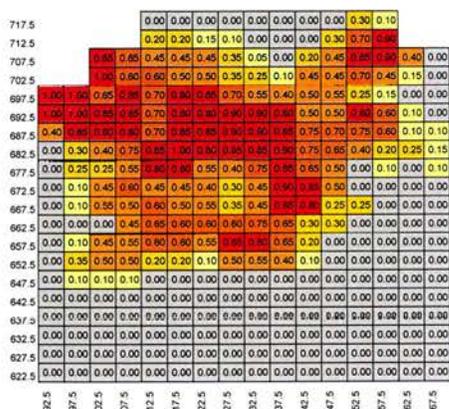
Changing the scale over which A-SSj values were computed also changes the number of data points, as seen in Figure 5.3.2.2, and so makes comparison more subjective. As may be expected, when computed over a 5m radius median A-SSj values appear more patchily distributed to those calculated over a 10m radius and are lower in value. In contrast median A-SSj values calculated over a 20m radius are more uniform in distribution and generally higher in value. In addition, A-SSj-PTC values increase with scale. Similarly, I-SSj values are



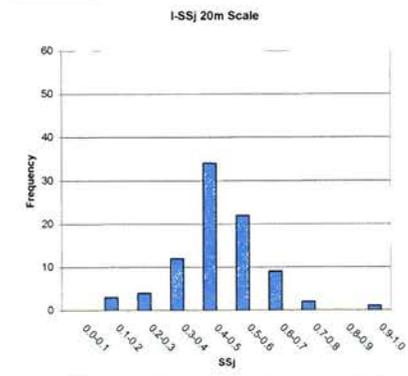
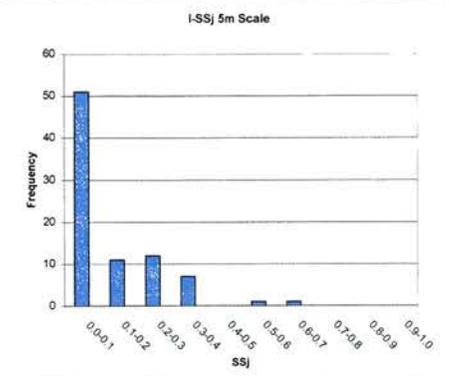
(a) Frequency distributions of median A-SSj values



(b) Geographical distributions of median A-SSj values



(c) Geographical distributions of median SSj-PTC values



(d) Frequency distributions of median I-SSj values

Figure 5.3.2.2. Distributions of median A-SSj, A-SSj-PTC and median I-SSj values calculated at 5m and 20m radii (b)-(c) Axes represents OSGB eastings (prefix 181\*\*\*) and northings (prefix 1032\*\*\*). Map units are in metres.

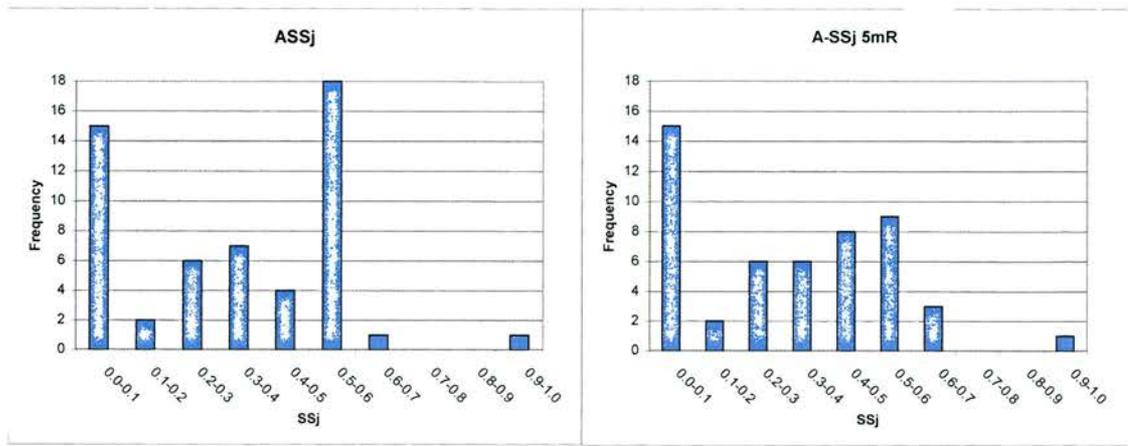
lower than those calculated at 10m when calculated at 5m (Wilcoxon:  $n=83$ ,  $Z=-7.384$ ,  $p<0.05$ ) and higher when calculated at 20m (Wilcoxon:  $n=83$ ,  $Z=-7.282$ ,  $p<0.05$ ). While I-SSj values at a 20m scale are correlated with those calculated at 10m, I-SSj values calculated at a 5m scale are not (Partial Mantel. 10m-5m:  $n=83$ ,  $Mcoeff=0.1128$ ,  $p=0.07$ ; 10m-20m:  $n=83$ ,  $Mcoeff=0.4162$ ,  $p<0.05$ ).

#### Spatial effects: Grid placement

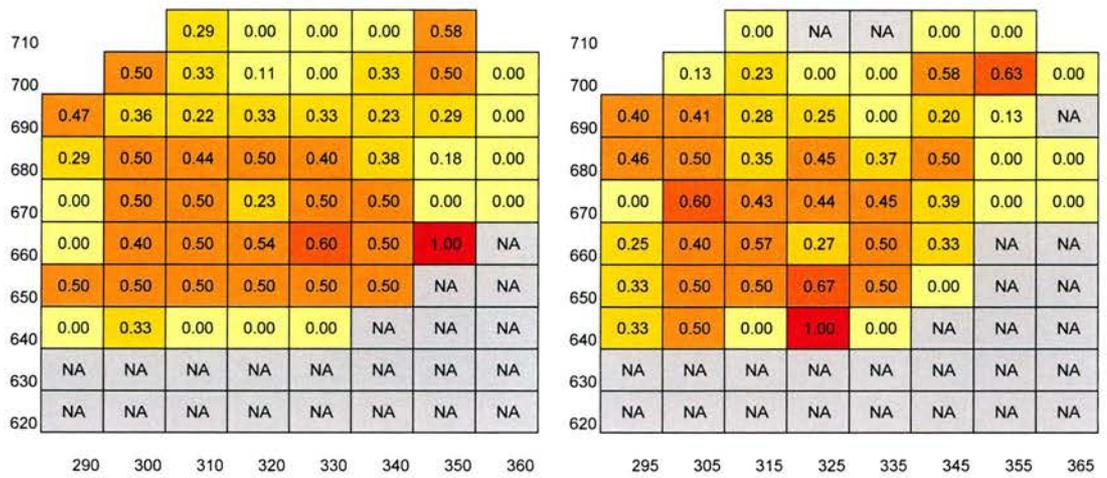
Shifting the locations around which to calculate A-SSj values produces a data set that is also difficult to compare to standard due to the spatial structure present. Table 5.3.2.2 shows no distinguishable difference in quartile values. Figure 5.3.2.3 shows similar geographical distribution of A-SSj values in comparison to standard, however it is clear that there are some differences. It is important to note that these two data sets, although similar, constitute two different areas.

#### Temporal Effects: Inter-survey interval

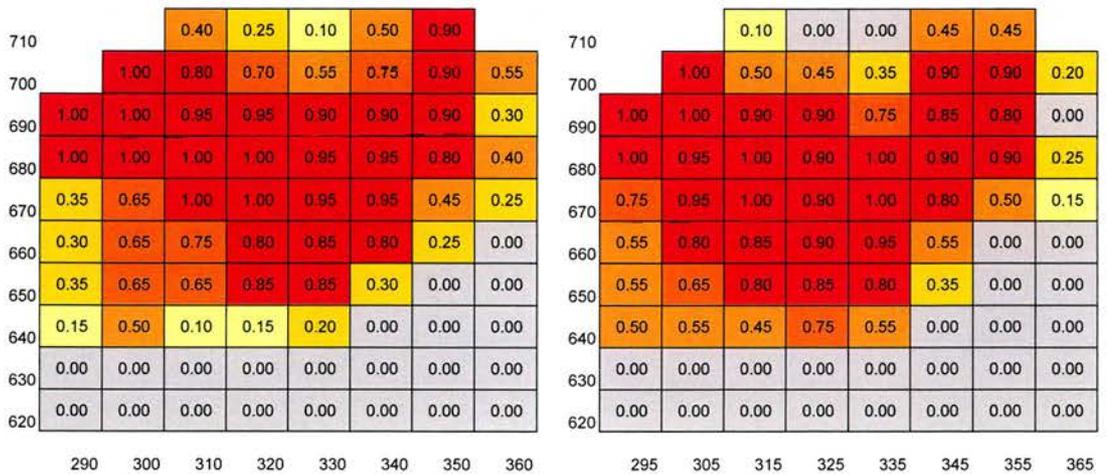
The time interval between surveys was irregular, ranging between 1 and 4 days with a mean of 1.7 days in 2002. Restricting the data to 5 surveys (2,7,11, 15 and 21), each 8 days apart, produced the minimum regular pattern available in the data. In 2003 time intervals ranged between 1 and 5 days with a mean of 1.8 days. Restricting the data to 4 surveys (2,7,13 and 19), each 11 days apart, produced the minimum regular pattern available in the data. This produced clearly depressed A-SSj values in comparison to standard as seen in Figure 5.3.2.4. In addition, A-SSj values decreased as the time interval over which they were calculated increased. Figure 5.3.2.5 shows this decrease of A-SSj values



(a) Frequency distribution of median A-SSj values



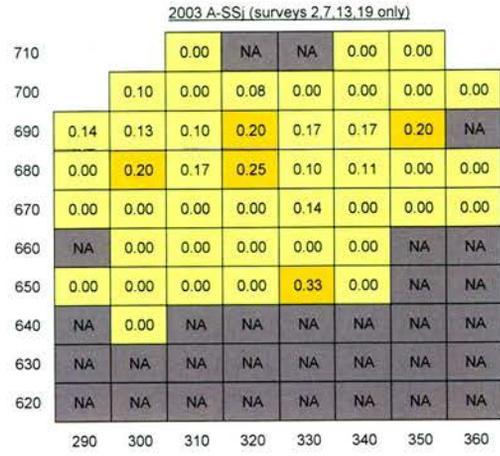
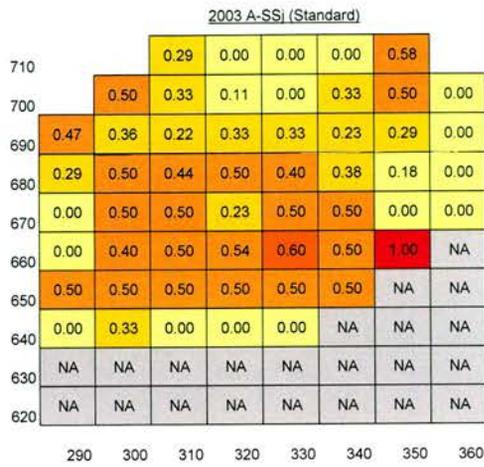
(b) Geographical distribution of median A-SSj values



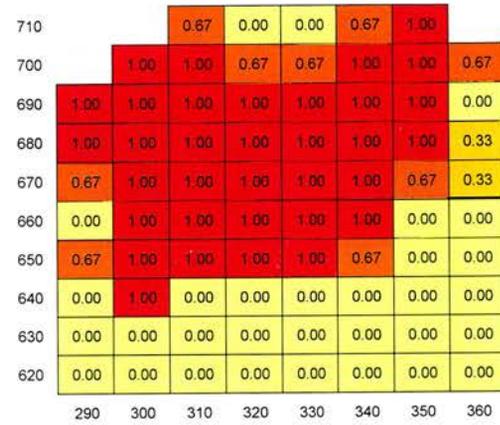
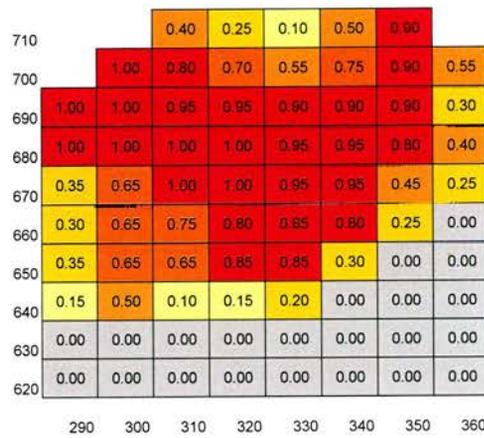
(c) Geographical distribution of median A-SSj-PTC values

Figure 5.3.2.3. Distributions of median A-SSj and A-SSj-PTC values calculated at Standard locations and shifted 5m to the right (east).

(b)-(c) Axes represents OSGB eastings (prefix 181\*\*\*) and northings (prefix 1032\*\*\*). Map units are in metres.



(a) Geographical distribution of median A-SSi values



(b) Geographical distribution of median A-SSi-PTC values

Figure 5.3.2.4. Geographical distributions of median A-SSi values calculated as standard and with the minimum standard inter-survey interval of 11 days.

Axes represents OSGB eastings (prefix 181\*\*\*) and northings (prefix 1032\*\*\*). Map units are in metres.

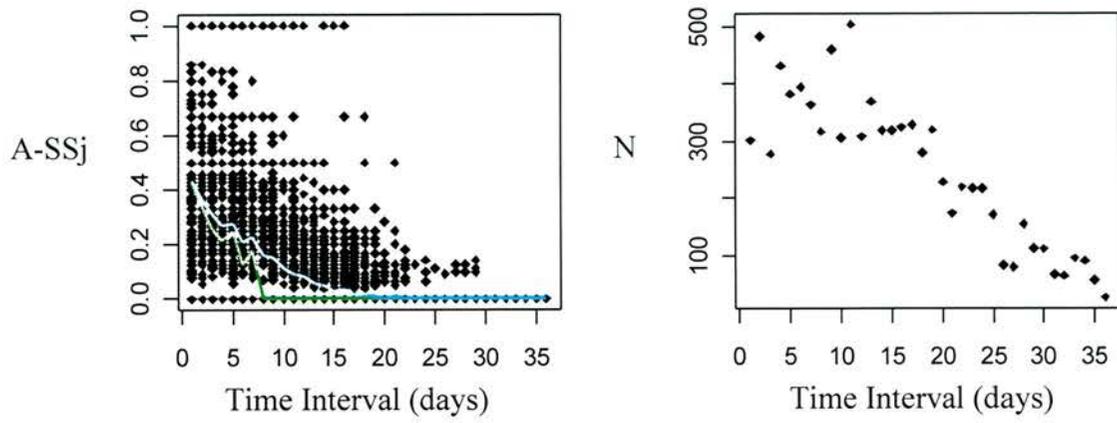


Figure 5.3.2.5. A-SSj and sample size (N) plotted against inter-survey time interval. The blue line represents the **mean** A-SSj value for each time interval and the green line represents the **median** value for each time interval.

with increasing time interval and the number of data points available for each time interval.

### 5.3.3 Discussion

The effect of missing data is a worry for any study, and understanding the effect that data would have should it not be missing is obviously impossible. However, it is not impossible to investigate the likely effect of this data given knowledge of the system in question. In this section the effect of giving identity to unidentified animals was investigated. Assigning all missing data to 'as new' status is perhaps not the most likely situation but it is certainly possible. This caused a depression in social stability values. A downward shift in both A-SSj and I-SSj values under this condition is logical as social stability is diluted by the extra influx of individuals. Reassigning missing data by a process akin to making the 'best guess' of who unidentified animals might be may seem overly speculative but is in fact probably the most realistic condition. This is because missing data was not due to the appearance of unknown animals, but to poor quality photographs and inability to identify individuals in the field. This may be due to an obstruction in the field of view, dirty or dry pelage, extreme angle of orientation or any combination of the above (Chapter 2.3.3). To be unidentified it would be necessary for an individual to remain in that state for the duration of observations on that day. It would seem reasonable to suggest that newcomers may appear all the more conspicuous as they are cleaner than those that have been on shore for some time (pers. obs.). In addition, females are more active towards the beginning of lactation, further aiding in identification (Boness et al., 1982; Redman, 2002). It is logical also then that I-SSj values increase under this

reassignment condition as social stability is bolstered by the increased immobility of resident animals. Crucially, however, there is a high correlation between all treatments of missing data and Standard, suggesting that the patterning of social stability values (whether they are increased or decreased in general) is similar. This study therefore seems adequately robust to the level of missing data encountered. It is likely that this is due to data being missing uniformly in time and space.

Changing the scale over which associations are defined has a dramatic effect on the resultant description of social structure. Definitions of association vary widely depending on context, from actual interaction to group membership or spatial and temporal proximity (Whitehead & Dufault, 1999). Changing the scale over which social stability was calculated (and so the definition of association) changed the results in a predictable manner, an increase in resolution providing a more patchy distribution and a decrease in resolution providing more uniformity. Although there is this potential for alternative results given scale there is confidence that the study has been carried out with a suitable definition of association. As bottlenose dolphins are likely to interact if in the same pod (Chilvers & Corkeron, 2002) and American Bison are likely to interact or coordinate movement if within 90m (Lott & Minta, 1983), female grey seals are likely to at least be aware of others within 10m on the breeding ground but are unlikely to interact with those further away (Chapter 3).

When A-SSj calculations were shifted by 5m a map was produced of similar pattern but alternative detail to Standard. This is expected as each area is unique in comparison to Standard and the individuals comprising the data for each calculation are different. A similar pattern and variability in A-SSj provides

support for the effectiveness of this measure in quantifying spatially defined social stability at the chosen scale.

The effect with the most serious consequences was that of variation in time interval between surveys. The temporal resolution available from subsampling the data to keep time interval constant was too coarse to provide information on within season social stability that would affect individuals. As time interval increased, social stability decreased. Mean social stability levelled off to zero at around 21 days interval. It follows that social stability would unlikely be above zero after 21 days as most mothers abandon their pup at this time, leaving to mate and return to the sea (Pomeroy et al., 1999). The implications of this decrease in social stability over time are of importance if social stability values are to be compared. It may not make sense to compare values that have been calculated over different intervals. For instance, care must be taken when comparing I-SSj values attributed to individuals that were present on the colony at different times. This is not an issue, however, when time intervals are identical, such as in the case of within year A-SSj values or comparison of observed values against the null model presented in the next section.

## 5.4 Null model simulation of seal behaviour

### 5.4.1 Methods

Description of the social environment on North Rona has provided evidence of considerable variation in the social stability both within areas and experienced by individuals. However, only if the observed social stability differs from that expected by chance would there be evidence of active social behaviour. Tests for active sociality are often carried out by comparison with random null model simulations in which important features of the original data are retained (Bejder et al., 1998; Whitehead, 1999). It is necessary to constrain the simulation in order to provide a realistic representation of seal behaviour that is only deficient in the parameter under study: the ability to respond to social stimuli.

There are three core parameters, other than sociality, that characterise female seal behaviour on North Rona: temporal residence, movement and site choice. Female grey seals move only over small ranges during their limited time of stay on the colony (Pomeroy et al., 1999, Chapter 2). Female grey seals are also known to prefer areas of certain topographic quality (Twiss et al., 2000). The simulation presented here is constrained by these three parameters in the following ways. The presence or absence of seals in the simulation mirrors exactly that of the observed data in both years. In this way the temporal patterning of maternal attendance does not differ from reality. Seals within the simulation could only occupy locations that were observed to be occupied in the year under test. Site choice within the simulation was therefore constrained to suitable habitat. Movement distances within the simulation were taken from the observed distribution of inter-survey movements. In this way movement was

also constrained to mirror that which was actually observed. The only core parameter in which the simulation can differ from reality is therefore in active coordination of proximity between individuals.

The simulation must be carried out many times in order to provide a distribution of expected values against which to test the observed. Five thousand permutations were chosen as this is in line with other studies and is the suggested quantity against which to test behaviour through randomisation procedures (Adams & Anthony, 1996; Bejder et al., 1998; Whitehead, 1999).

The structure of the simulation is akin to an individual based model with Monte Carlo randomisation techniques directing behaviour. The simulation was carried out using the functions "newsim\_possxy.fn", "distance.fn", "newsim\_pdf.fn" and "newsim.fn9" (detailed in Appendix A.4.1-A.4.4) written by the author for this study in R (R Development Core Team, 2004). The set of all observed locations (Figure 5.4.1.1(a)) and probability of movements (Figure 5.4.1.1(b)) were unique for 2002 and 2003.

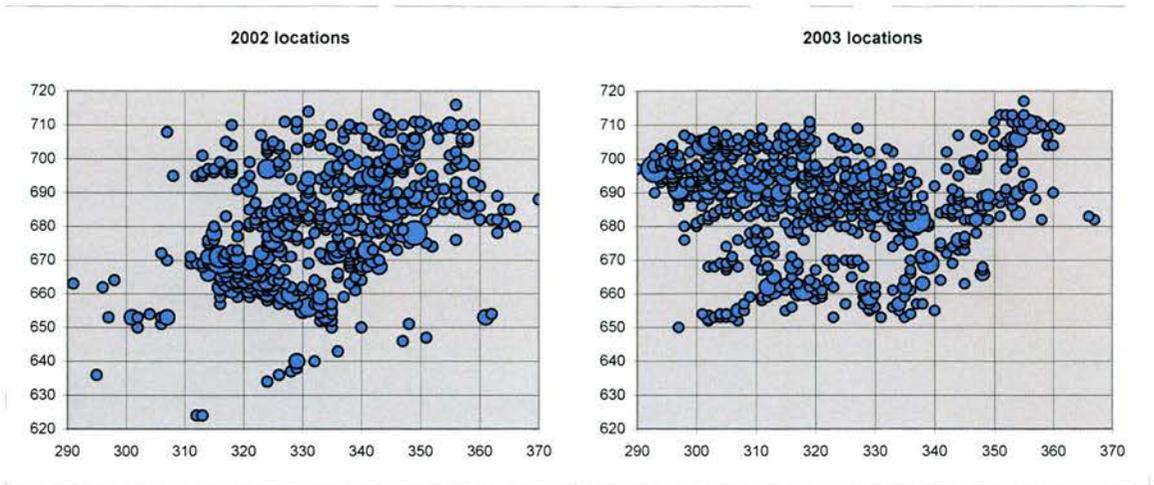
#### Simulation procedure (x5000)

For each survey:

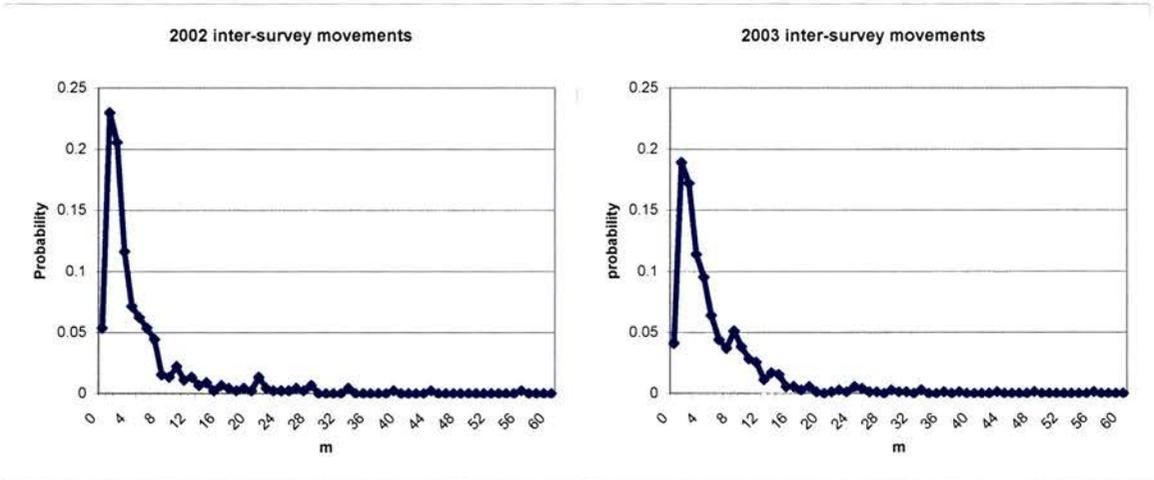
1. Animal presence mirrors that of observed.
2. On first survey locations are unaltered from observed.
3. On each subsequent survey a new location was allocated to each individual present.

For each individual present:

1. On first survey in which an individual was observed, a location was allocated from the pool of all observed locations.



(a) All observed locations used (size of bubble denotes number of times used)



(b) Observed movement probability distributions

Figure 5.4.1.1. Locations used and inter-survey movement probabilities observed in 2002 and 2003  
 (a) Axes represents OSGB eastings (prefix 181\*\*\*) and northings (prefix 1032\*\*\*). Map units are in metres.

2. On subsequent surveys a new location was allocated from the pool of all observed locations, weighted by the probability of moving to each location by the observed probability distribution of movements.

The output of each simulation run was a new data set containing new locations for each animal on each day that it was present. A-SSj and I-SSj values were then calculated for each area and each individual and summarised over the (simulated) season by the median. After 5000 permutations a distribution of median A-SSj and I-SSj values was available for each area and individual.

Wilcoxon and Mantel procedures were used as before to provide global tests of differences between observed and simulated SSj values. Simulated values were tested for any general increase or decrease in SSj values in comparison to observed. Wilcoxon tests were used to compare observed A-SSj and I-SSj values against the median A-SSj and I-SSj values from the simulated distributions. In addition, Mantel tests were used to compare the spatial patterning of observed A-SSj values to the median values from simulated distributions. As individuals were necessarily occupying different locations in the simulation to those they occupied in reality, the spatial structure of I-SSj values was not compared.

In addition, the distribution of median SSj values for each area and individual provides a unique test of significance of observed against simulated values. These constitute local tests for differences between observed and simulated SSj values. It was not known whether observed SSj values would be higher or lower than chance and so a two tailed test was employed. Using an alpha criterion of 0.05, each observed A-SSj and I-SSj value was assessed as

being significantly different to chance if it fell within the upper or lower 0.025% tails of its respective simulated distribution. As this involved many tests of significance a Bonferroni correction was also applied ( $\alpha = 0.025$  divided by the number of A-SSj or I-SSj tests in each year).

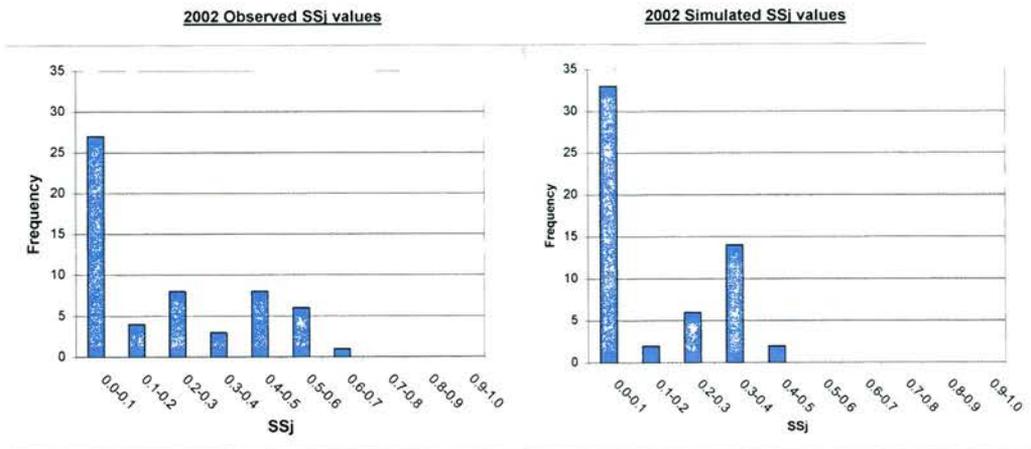
#### 5.4.2 Results

##### Global tests of A-SSj

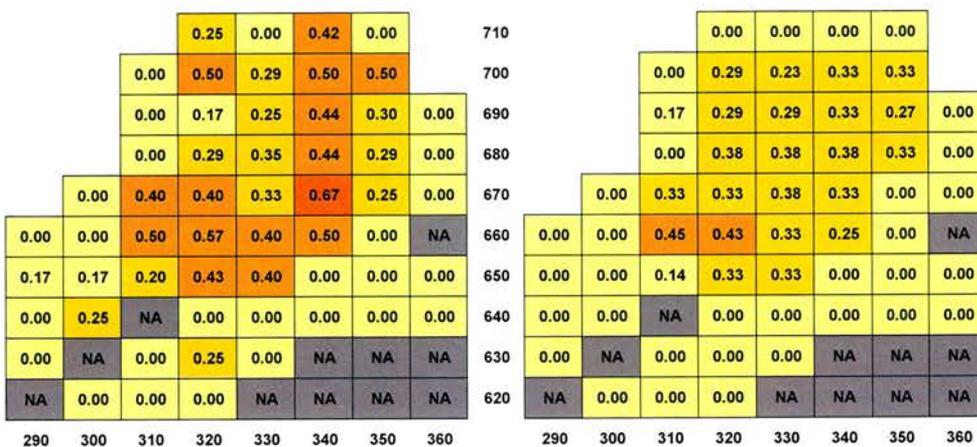
In both 2002 and 2003 simulated A-SSj values had a smaller range and were more uniform in spatial distribution than observed (Figures 5.4.2.1 and 5.4.2.2). Observed A-SSj values were higher than the median simulated values in 2002 and 2003 (Wilcoxon. 2002:  $n=57$ ,  $Z=-3.57$ ,  $p<0.05$ ; 2003:  $n=54$ ,  $Z=-3.85$ ,  $p<0.05$ ). Median simulated A-SSj values were correlated with observed values in 2002 and 2003 (Partial Mantel. 2002:  $n=57$ ,  $Mcoef=0.68$ ,  $p<0.05$ ; 2003:  $n=54$ ,  $Mcoef=0.36$ ,  $p<0.05$ ). Therefore, although observed values of A-SSj were higher than simulated, the spatial patterning of values was the same.

##### Global tests of I-SSj

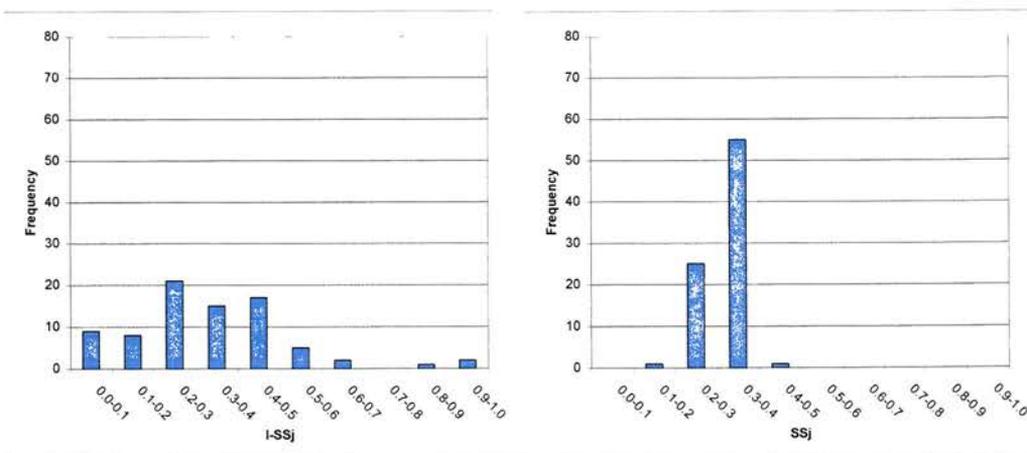
The distribution of simulated I-SSj values had a smaller range than observed values, but were similar in central tendency (Figures 5.4.2.1(c) and 5.4.2.2(c)). Observed I-SSj values were neither generally elevated nor generally depressed in comparison to median simulated values in 2002 or 2003 (Wilcoxon. 2002:  $n=80$ ,  $Z=-0.86$ ,  $p>0.05$ , 2003:  $n=86$ ,  $Z=-1.88$ ,  $p=0.06$ ). The p-value verges on significance for 2003 however, indicating a possible trend for higher observed I-SSj values than simulated in this year. Because this was a paired-sample comparison, observing no general shift to higher or lower I-SSj values does not



(a) Frequency distributions of median A-SSi values



(b) Geographical distributions of median A-SSi values

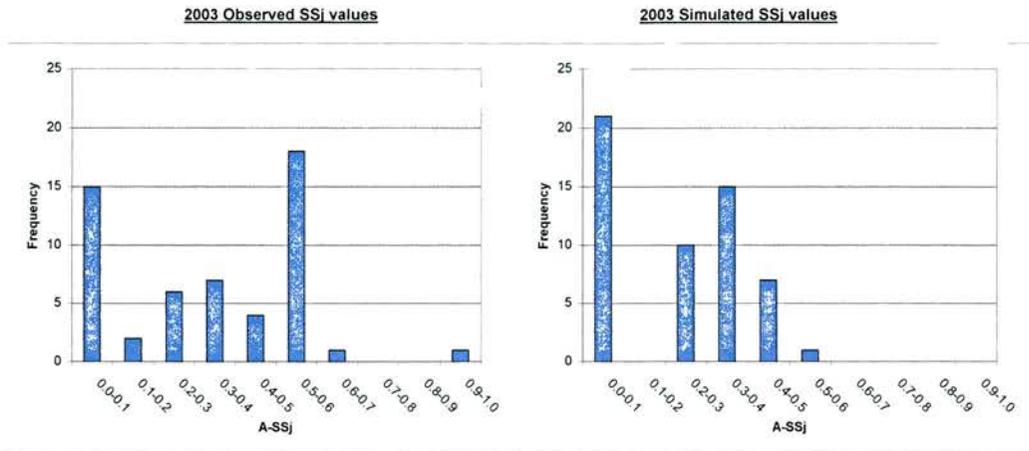


(a) Frequency distributions of median I-SSi values

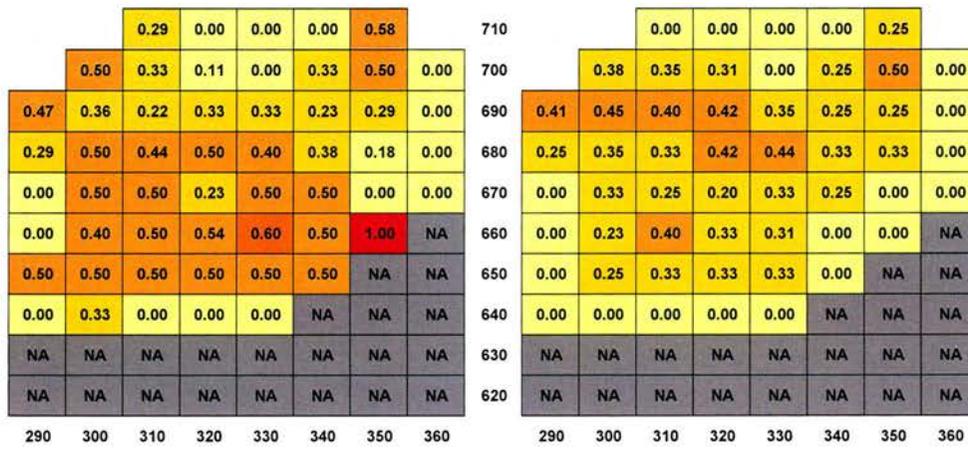
Figure 5.4.2.1. Distributions of observed and simulated median A-SSi and I-SSi values in 2002

Simulated values are median values for each area or individual from 5000 iterations of the simulation.

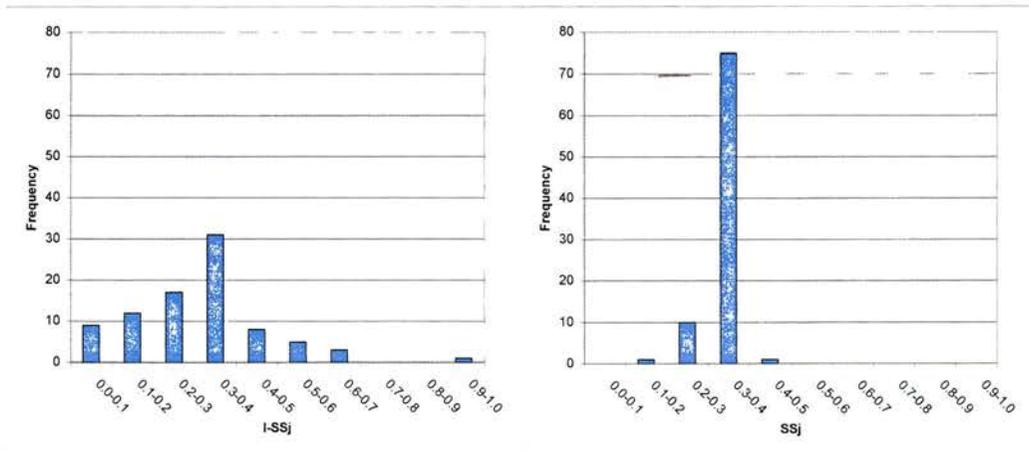
(b) Axes represents OSGB eastings (prefix 181\*\*\*\*) and northings (prefix 1032\*\*\*\*). Map units are in metres.



(a) Frequency distributions of median A-SSj values



(b) Geographical distributions of median A-SSj values



(a) Frequency distributions of median I-SSj values

Figure 5.4.2.2. Distributions of observed and simulated median A-SSj and I-SSj values in 2003

Simulated values are median values for each area or individual from 5000 iterations of the simulation.

(b) Axes represents OSGB eastings (prefix 181\*\*\*) and northings (prefix 1032\*\*\*). Map units are in metres.

mean that observed values were no different to simulated. It is possible that roughly equal numbers of mothers experienced elevated levels of I-SSj as did experience lower levels of I-SSj than would be predicted by the model, a finding of equal importance. This is discussed further below.

#### Local tests of A-SSj

In accordance with the Wilcoxon tests above, there were more areas in which observed A-SSj was higher than simulated than were lower than simulated in 2002 (Figure 5.4.2.3) and 2003 (Figure 5.4.2.4). In 2002 there were 24 locations in which observed A-SSj was greater than simulated (green outline), 7 in which observed was less than simulated (red outline) and 26 in which there was no difference (black outline). Similarly, in 2003 there were 29 locations in which observed A-SSj was greater than simulated, 9 in which observed was less than simulated and 16 in which there was no difference.

Locations that were used less by animals also had fewer simulated A-SSj values and therefore less power to test for a difference between observed and simulated values. There were two locations of significantly higher observed A-SSj than chance in 2002. Location (320,660) at the standard two-tailed level of significance (blue bars) and location (340,670) at the Bonferroni corrected level of significance (black bars). In 2003, two locations were associated with higher observed A-SSj values than simulated, (320,660) and (330,660) and one with lower observed A-SSj values than simulated, (310,690), all at the standard level of significance.

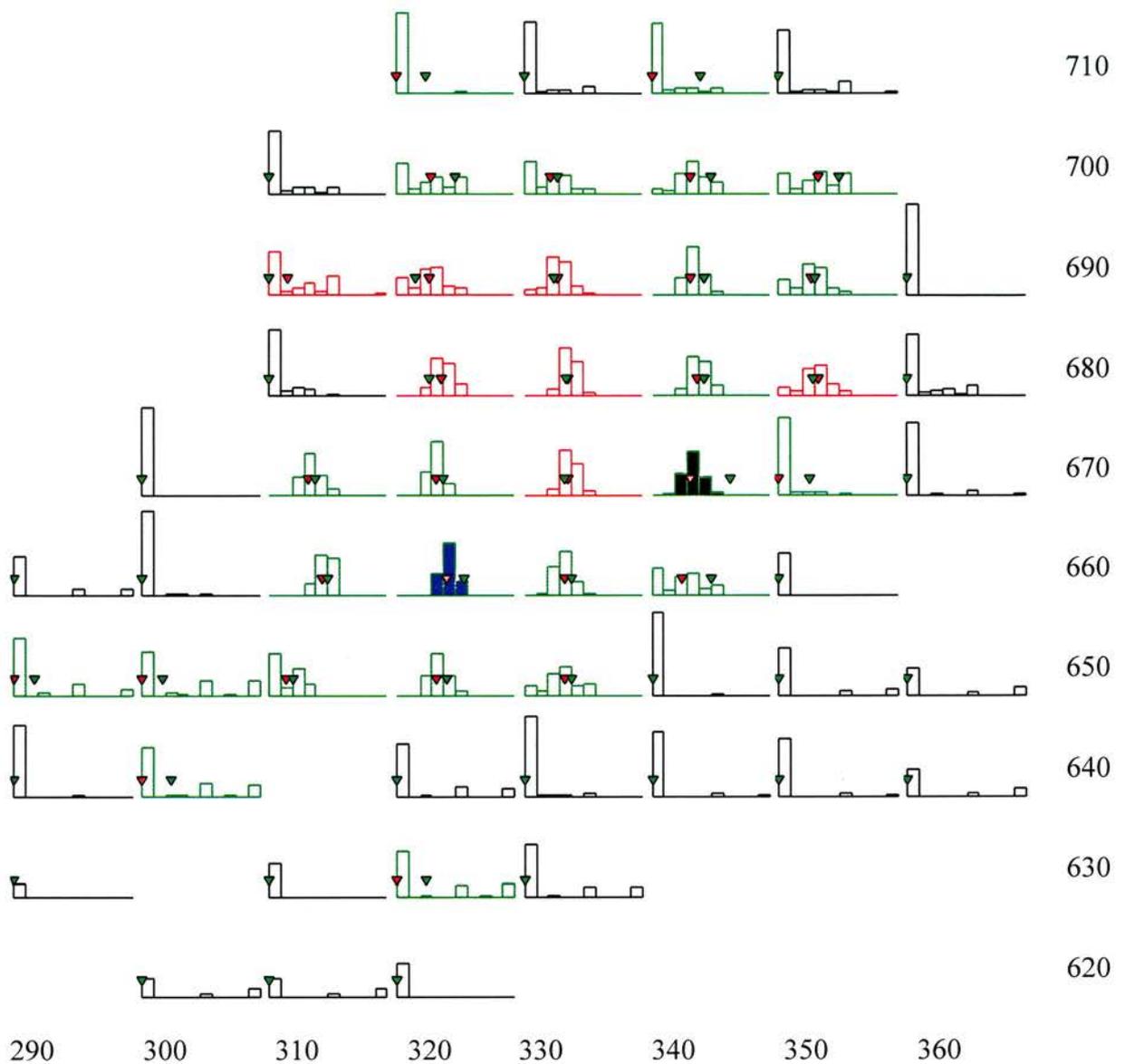


Figure 5.4.2.3. Distributions of simulated median A-SSj values in 2002.

Histograms display the median simulated values from 5000 simulations, plotted in a representation of real world locations. Axes represents OSGB eastings (prefix 181\*\*\*) and northings (prefix 1032\*\*\*). Map units are in metres. The observed A-SSj value for each location is plotted as a green triangle and the median simulated value as a red triangle. Black, green and red outlines denote where observed values are equal to simulated, are greater than simulated, and are less than simulated respectively. Grey bars denote where observed values are not significantly different to simulated values. Blue bars denote where observed values are significantly different to simulated values at standard 2-tailed  $\alpha = 0.025$ . Black bars denote where observed values are significantly different to simulated values at Bonferroni adjusted 2-tailed  $\alpha = 0.025/\text{number of tests}(57)$ .

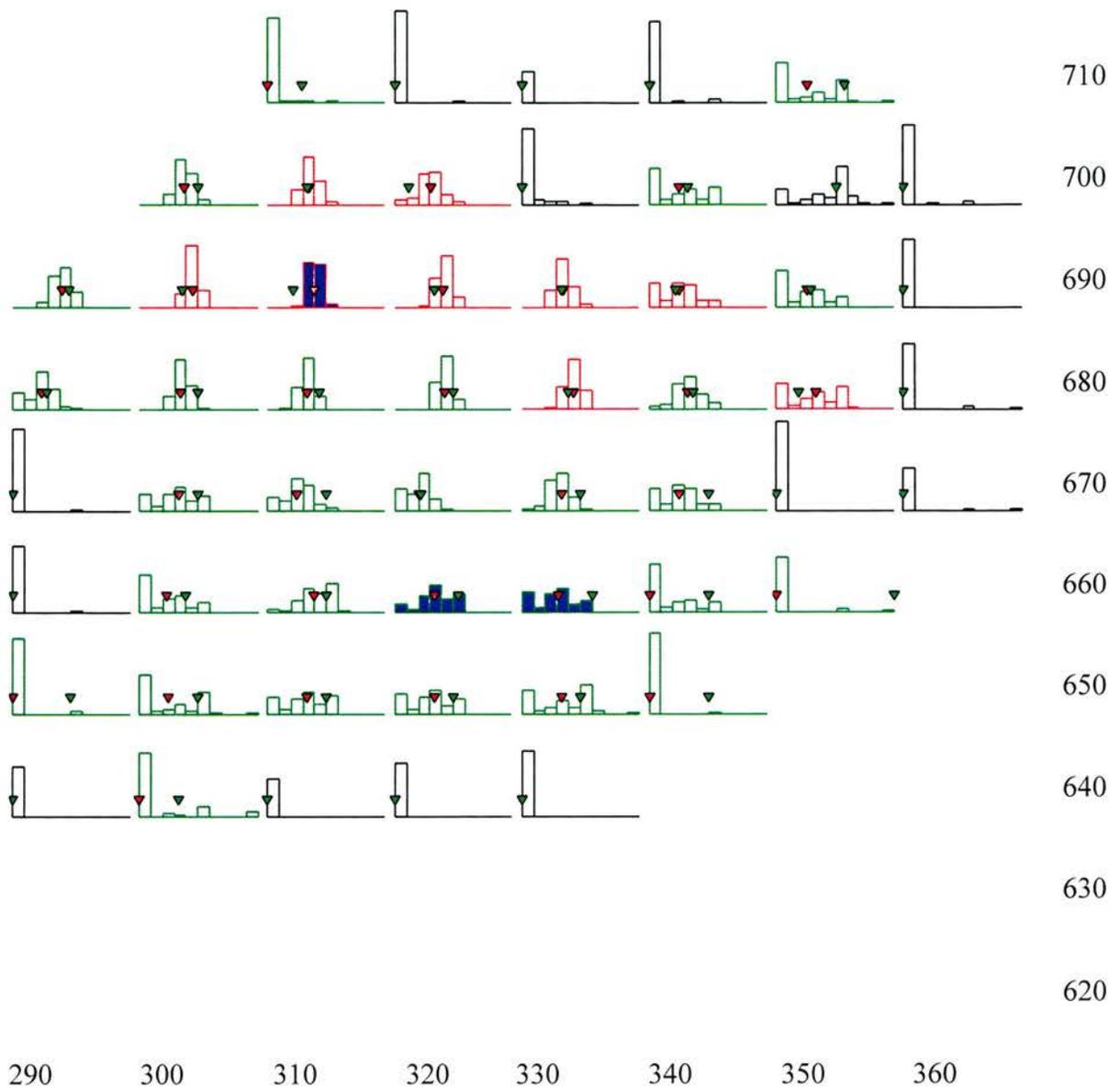


Figure 5.4.2.4. Distributions of simulated median A-SSj values in 2003.

Histograms display the median simulated values from 5000 simulations, plotted in a representation of real world locations. Axes represents OSGB eastings (prefix 181\*\*\*) and northings (prefix 1032\*\*\*). Map units are in metres. The observed A-SSj value for each location is plotted as a green triangle and the median simulated value as a red triangle. Black, green and red outlines denote where observed values are equal to simulated, are greater than simulated, and are less than simulated respectively. Grey bars denote where observed values are not significantly different to simulated values. Blue bars denote where observed values are significantly different to simulated values at standard 2-tailed alpha = 0.025. Black bars denote where observed values are significantly different to simulated values at Bonferroni adjusted 2-tailed alpha = 0.025/number of tests(54).

Local tests of I-SSj

In accordance with the Wilcoxon tests, observed I-SSj values were neither generally higher nor lower than the models predictions in 2002 or 2003 as roughly equal numbers of individuals experienced elevated I-SSj values in comparison to the simulation as did experience lower I-SSj values. In 2002 there were 42 individuals with observed I-SSj values greater than simulated (green outline), 38 with observed values less than simulated (red outline) and 2 with no observed value available (black outline). This last instance occurs when observed individuals do not have any neighbours within the 10m search radius in reality, but do in the simulation. Any I-SSj value from the simulation will therefore be higher than the record of no observed sociality. In 2003, 38 individuals were associated with observed I-SSj values greater than simulated, 48 with observed less than simulated and 1 with no observed value available.

Some individuals therefore experienced significantly higher I-SSj than simulated and some experienced significantly lower I-SSj than simulated. There were 11 cases in 2002 where individuals had I-SSj values that were significantly different to the models predictions. Two of these were robust to Bonferroni correction (black bars), both of which were those individuals for which observed I-SSj values were not available. This is because in the simulation, these individuals had animals within the 10m search radius, whereas in reality they did not. Of the remaining 9 at the standard level of significance 7 cases involved individuals with greater I-SSj values than simulated and 2 cases involved individuals with lower I-SSj values than simulated. In 2003 there were three cases in which observed I-SSj values were higher than simulated at the standard

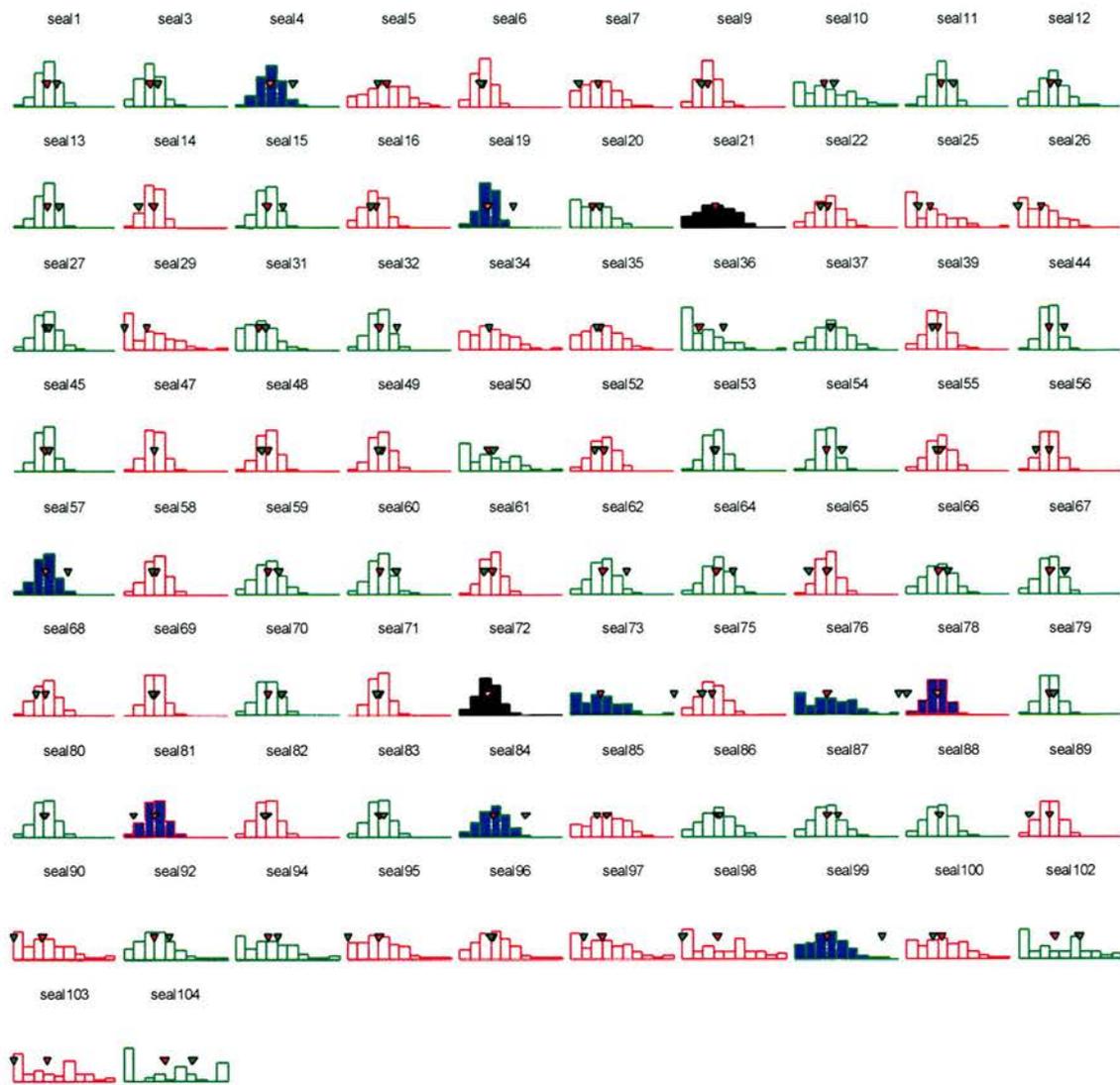


Figure 5.4.2.5. Distributions of simulated median I-SSj values in 2002.

Histograms display the median simulated values from 5000 simulations for each individual (Individuals that were ephemeral in the study area and for which no I-SSj value was available were omitted). The observed I-SSj value for each individual is plotted as a green triangle and the median simulated value as a red triangle. Black, green and red outlines denote where observed values are equal to simulated, are greater than simulated, and are less than simulated respectively. Grey bars denote where observed values are not significantly different to simulated values. Blue bars denote where observed values are significantly different to simulated values at standard 2-tailed  $\alpha = 0.025$ . Black bars denote where observed values are significantly different to simulated values at Bonferroni adjusted 2-tailed  $\alpha = 0.025/\text{number of tests}(82)$ .

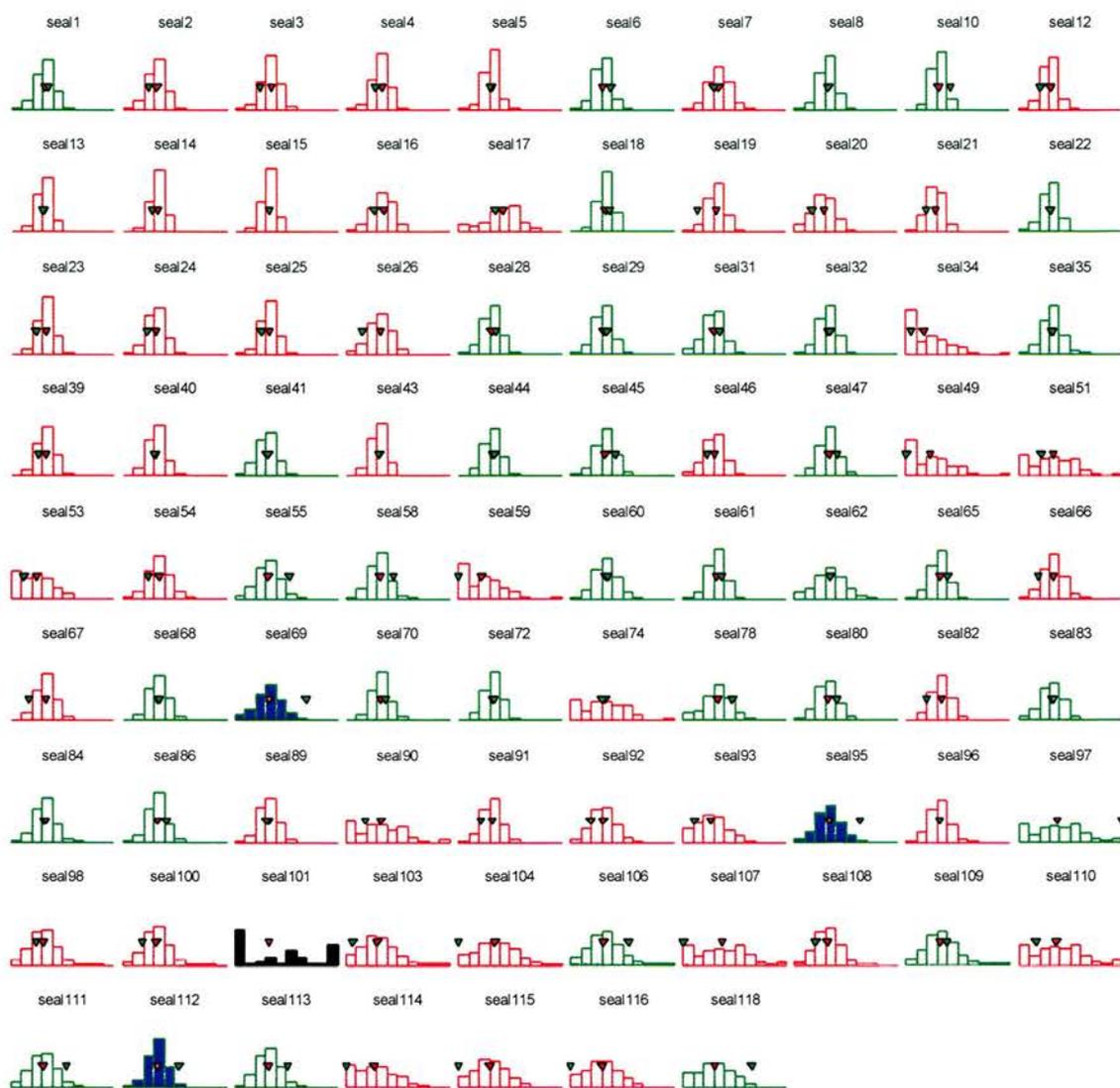


Figure 5.4.2.6. Distributions of simulated median I-SSj values in 2003.

Histograms display the median simulated values from 5000 simulations for each individual (Individuals that were ephemeral in the study area and for which no I-SSj value was available were omitted). The observed I-SSj value for each individual is plotted as a green triangle and the median simulated value as a red triangle. Black, green and red outlines denote where observed values are equal to simulated, are greater than simulated, and are less than simulated respectively. Grey bars denote where observed values are not significantly different to simulated values. Blue bars denote where observed values are significantly different to simulated values at standard 2-tailed  $\alpha = 0.025$ . Black bars denote where observed values are significantly different to simulated values at Bonferroni adjusted 2-tailed  $\alpha = 0.025/\text{number of tests}(87)$ .

level of significance and one case in which an observed I-SSj value was lower than simulated at the Bonferroni corrected level of significance.

The global Wilcoxon test did not pick up any difference between observed and simulated I-SSj values as this test assess for general upwards or downwards shifts in values. It appears, however, that as many individuals experienced reduced I-SSj in comparison to the simulation as experienced elevated I-SSj. Some of these tests were significant themselves, highlighting the importance of carrying out both global and local tests. Table 5.4.2.1 summarises the significant simulation results. Location (320,660) was associated with elevated levels of social stability in both 2002 and 2003. All 4 individuals with low I-SSj values in 2002 were located towards the periphery of the study area and away from the main groups of animals. Of these animals Seal 81 from 2002 was present again as Seal 69 in 2003. This individual had lower than simulated social stability in 2002 and although being in a similar location, higher than simulated social stability in 2003. Animals that did not raise a pup in the study area were perhaps subject to different constraints to those that did and as such different levels of I-SSj may be expected. The simulation did not differentiate between breeders and non-breeders. Also, animals for which there are only a limited number of I-SSj values available are perhaps more prone to outlying values.

### 5.4.3 Discussion

The null model of seal behaviour shows increased uniformity in comparison to observed values of social stability. Simulated A-SSj values were

**Table 5.4.2.1. Summary of within year SSj observations that were significantly different to those from simulation.**

↑ denotes observed SSj values greater than simulated. ↓ denotes observed SSj values lower than simulated. x denotes non significance.

SSj sim: simulated median SSj value. SS-j obs: observed median SSj value. Surveys Occ/Pres: number of surveys in which location was occupied / animal was present  
 SSj-PTC: proportion of time over which SSj was computable. S: total number of individuals within 10m. Centroid: centroid location for individual

2002 A-SSj

Location	Standard 2-tailed	Bonferroni 2-tailed	A-SSj Sim	A-SSj Obs	Surveys Occ.	A-SSj-PTC	S
320,660	↑	x	0.43	0.57	22	1.00	32
340,670	↑	↑	0.33	0.67	21	1.00	19

2002 I-SSj

Animal	Standard 2-tailed	Bonferroni 2-tailed	I-SSj Sim	I-SSj Obs	Surveys Pres.	I-SSj-PTC	S	Centroid	Notes
Seal 4	↑	x	0.34	0.56	8	1.00	18	324,661	
Seal 19	↑	x	0.28	0.53	12	1.00	24	319,669	
Seal 21	↑	↓	0.33	NA	5	0.00	6	355,709	NE periphery. Only 2 poss SSj values.
Seal 57	↑	x	0.31	0.54	9	1.00	16	333,655	
Seal 72	↑	↓	0.28	NA	7	0.00	0	361,653	SE periphery on own.
Seal 73	↑	x	0.29	1.00	5	1.00	1	306,653	SW periphery. Only 1 poss SSj value
Seal 76	↑	x	0.31	1.00	2	1.00	1	291,663	SW periphery. Only 1 poss SSj value. No pup observed
Seal 78	↑	x	0.30	0.00	8	0.17	1	328,638	S periphery on own
Seal 81	↑	x	0.30	0.09	8	1.00	10	349,710	= Seal 69 in 2003; North periphery
Seal 84	↑	x	0.33	0.64	10	1.00	8	338,672	
Seal 99	↑	x	0.31	0.83	7	1.00	2	340,669	

2003 A-SSj

Location	Standard 2-tailed	Bonferroni 2-tailed	A-SSj Sim	A-SSj Obs	Surveys Occ.	A-SSj-PTC	S
310,690	↑	x	0.40	0.22	18	0.95	44
320,660	↑	x	0.33	0.54	15	0.80	11
330,660	↑	x	0.31	0.60	17	0.85	10

2003 I-SSj

Animal	Standard 2-tailed	Bonferroni 2-tailed	I-SSj Sim	I-SSj Obs	Surveys Pres.	I-SSj-PTC	S	Centroid	Notes
Seal 69	↑	x	0.33	0.69	6	1.00	4	355,705	= Seal 81 in 2002
Seal 95	↑	x	0.33	0.63	9	1.00	14	295,696	
Seal 101	↑	↓	0.33	NA	4	0.00	9	344,685	no pup; only 1 poss SSj value; came and went
Seal 112	↑	x	0.33	0.54	10	1.00	19	335,682	

generally lower, while simulated I-SSj values were generally more moderate. This does suggest that animals operating without social influence would be behaving differently to the animals observed. However, there is still variability in the simulation output suggesting that other pressures may also have an effect on social stability. This is investigated further in the next section of this chapter. Observed A-SSj was greater than or equal to simulated in most cases. However, in both years there was an area in which A-SSj was consistently lower than expected. This occurred in roughly the same location in both years and would appear to constitute a less socially favourable area in which to reside. In addition, there was an area that appeared in both years to be of particularly increased social stability suggesting the presence of a more socially favourable location. Individuals experience considerably different values of social stability to each other, roughly equal numbers having above or below I-SSj values than expected. Site choice and neighbour choice may therefore have a profound effect on the social stability that each mother experiences while raising her pup.

Only a handful of the deviations from the null model in A-SSj or I-SSj were statistically significant. This may be due to limitations within the simulation as opposed to the lack of a social effect. The simulation was designed to be as realistic as possible in representing seal behaviour (although devoid of the ability to respond to social stimuli) and as a result may be overly conservative. Clearly, a random relocation of animals without the constraints imposed in this model would have been excessively unrealistic, but striking a balance between simulation and replication of observed data is very difficult. Here, animals were only able to use locations and move distances from observed distributions. This was to encompass site and topography choice and to provide

realistic values for between survey movements. However, this observed data is taken from the very system that is under test and as such the observed behaviour may well be influenced by social factors. This means that there may be an inescapable amount of social dependency within the parameters of the simulation. If sociality does affect behaviour in the observed system, then locations used and distances travelled may be different to what would be expected in a non-social system. For instance, if social processes are serving to restrict movement and draw certain animals together then the location and movement distributions in the null model will be underestimated. A wider spread of available locations and an increase in the distance that individuals would be likely to move would most likely decrease the social stability output of the simulation and increase the number of significant deviations between observed and simulated values.

Randomisation based simulations have been used to test for non-random organisation in pair-wise association studies. Typically, for each iteration, a data pair from a presence/absence table are swapped so that the group membership of two animals is reversed for two observations (Bejder et al., 1998). Whitehead (1999) noted a lack of realism in this method in that animals could be reassigned to groups irrespective of the actual time periods in which they were observed. Two extensions to the method were proposed so that associations were only swapped within time periods and the number of associates that each animal had in each time period was kept constant. These constraints are akin to the limitations imposed in this study to make the simulation more realistic.

Global tests of general trends in  $SS_j$  values throughout the study area were carried out alongside local tests of  $SS_j$  values for specific locations and

individuals. In carrying out local tests it was necessary to compare only values unique to each area or individual under test. This is in comparison to testing the observed value for one locality against a summary of the simulated values at all localities. This is because each area or individual may have a different distribution of possible social stability values given factors such as topography and location. An area may therefore have a lower than average social stability value when compared to the study area as a whole, but this may not be different to that expected given its particular usage pattern.

Even though the simulation in this study erred on the conservative side, it is clear that there are differences between the observed and simulated values. Therefore, it appears that observed social stability values could not be explained fully by the model. Other than topography use and movement it is difficult to imagine what else might influence seal behaviour. Pups are able to move of their own accord and it is possible that if mothers were to move in response to this social stability may be affected. However, in general pups return to their mother and if mothers do follow their pups it is usually to guide them back to their original location (pers. obs.). The deviations of observed behaviour from that expected from this simulation suggest that some form of active social organisation may be driving the variety of social stability observed within the North Rona breeding rookery.

5.5 Multivariate analysis of factors affecting area-based social stability (A-SSj)

5.5.1 Methods

Predictors of A-SSj within the study area were investigated using spatial multivariate techniques. Spatial structure within the data must be taken into account because the assumption of independence required by standard statistical techniques is violated (Legendre, 1993). Spatial autocorrelation is present when data at one location is influenced by data at surrounding locations (Sokal & Oden, 1978). The danger, then, is that this form of pseudo-replication will lead to inflated degrees of freedom and inaccurate conclusions (Legendre, 1993). This can occur when spatial autocorrelation is present in the response or explanatory variables (Legendre et al., 2002). In addition, spatial structure is often an important component of the system being studied and so should be incorporated into the modelling process. In this case, it is clear that social stability at one location may well be influenced by social stability at a neighbouring location. This is exacerbated by the sampling process by which social stability is calculated, 10m radii around centres 10m apart necessarily overlapping. Mantel and partial Mantel tests have been used in previous sections to address this spatial structure in examining correlations between variable pairs. However, methods were not available to implement this technique on multivariate data (Rosenberg, 2004a). A variety of tools are available for the analysis of spatial data (see Dale et al., 2002; Perry et al., 2002), of which spatial regression is most suitable to this study (Anselin, 2002; Keitt et al., 2002). Spatial autocorrelation in the raw data is not necessarily a problem, so long as it is accounted for by covariates in the regression model. If, however, there is

spatial autocorrelation over and above that explained in the model then residual spatial autocorrelation may occur. Following the protocol in Anselin (Anselin, 2003a; Anselin, 2003b) it is possible to test for and address spatial autocorrelation in a linear modelling process using Bivand's package 'spdep' for R (Bivand et al., 2004; R Development Core Team, 2004). In this process a Moran's I statistic (Moran, 1950) is used to investigate spatial autocorrelation in the residuals of an ordinary least squares linear model. If residual spatial autocorrelation is present it can be addressed in two ways. Firstly, a spatially lagged weighting of the response variable can be incorporated as a new covariate in the regression. Secondly, a spatially lagged weighting in the error term can be included in the model. Application of a Lagrange multiplier (LM) test can then be used to find which of these alternative model specifications is most applicable (an RLM test, which is robust to the opposite specification being true, can also be used). A new model in which spatial dependence is incorporated into either the error term or as a new covariate based on the response variable, or both can then be proposed. Spatial structure is designated within this process by specifying neighbourhood lists over a given lag distance. A possible limitation of this approach is that the spatial weights included in the modelling process are only for those data points within the specified lag distance and are not a continuous function of distance. The choice of lag scale is therefore very important (Dungan et al., 2002). A lag distance of 10m (equating to rooks case adjacency and therefore specifying the pattern of overlap between A-SSj calculations at adjacent locations) was used here in accordance with the sampling regime and observed animal behaviour (Chapter 2). This implies that only spatial autocorrelation at a scale of 10m is of importance to this system.

Minimal linear models explaining A-SSj values in 2002 and 2003 were chosen by backwards stepwise selection through minimisation of AIC. The variables included in the model were reproductive synchrony, aggressive interactions, cost distance to pools of water, cost distance to the sea, elevation, slope and median density. Reproductive synchrony was calculated by dividing the observed standard deviation in birth dates by the maximum observable standard deviation in birth dates and subtracting from one. Therefore, if two animals within an area gave birth on the first and last days of observations, reproductive synchrony for that area would be 0. If, however, the two animals gave birth on the same day reproductive synchrony would be 1.

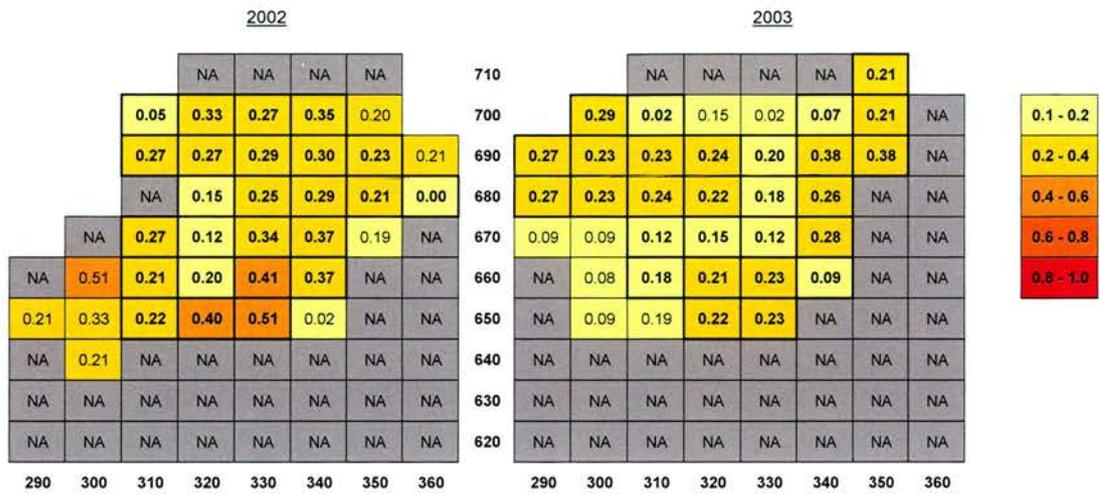
Aggressive interaction data was recorded differently in 2002 and 2003. In 2002 the study area was scanned at 5 minute intervals, locations of interactions being recorded within 10x10m grid cells. Ideally, scanning interval should be less than the duration of the behaviour under study (Martin & Bateson, 1986). This was not the case, however, as aggressive interactions were of short duration and typically lasted only a matter of seconds (Boness et al., 1982; pers. obs.). In 2003 continuous sampling of the entire study area was undertaken and interactions recorded with metre accuracy on a geo-rectified map. Aggressive interactions were counted as those between adult females and pups of greater severity than an alert response, including open mouth threats, clapping, flipping, lunging, biting and chasing (for further details on behavioural interactions see Chapter 2). Data from both years are provided as counts of interactions over seal days within grid cells in 2002 and at 10m radii around grid cell centres in 2003.

For information on the calculation of raw topography values including cost distance indices see Twiss et al., (2001) and Twiss et al., (2000). Cost

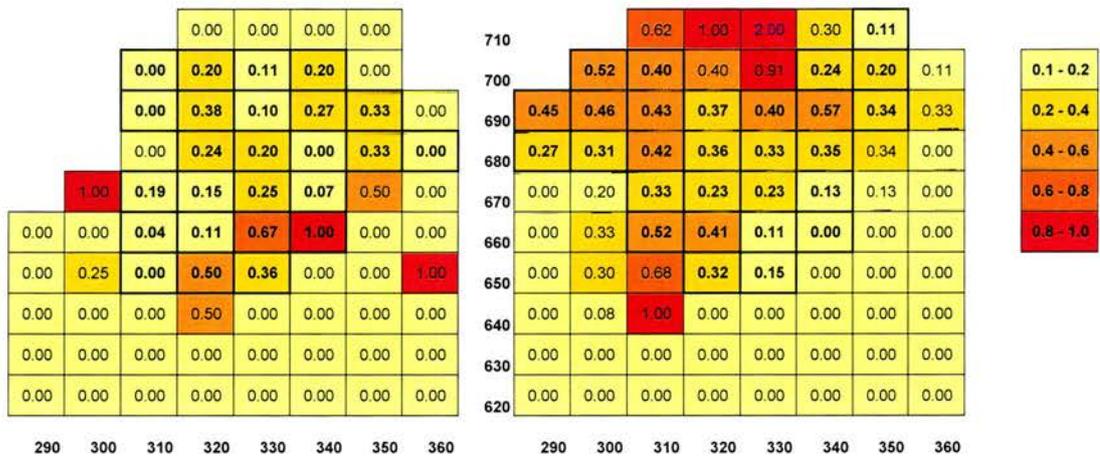
distance indices model the likely relative effort involved in moving from one location to another considering the nature of the terrain to be traversed and including the necessity to circumnavigate barriers. This is a more realistic representation of separation than straight line distance. Cost access to pool values were calculated from pool availability recorded on 21st October 1994. This date is the closest available to mid-way through the season and represents the main bodies of water and the most common pool availability that seals encounter. There was no significant difference between pool availability in 1994 and the years of study (Twiss, pers. comm.). All variables included in the modelling process (other than aggressive interactions in 2002) were resampled to provide medians at 10m radii around grid cell centres. Because not all A-SSj values were representative of the entire study period and so suffer from bias towards singular events it was not appropriate to include all data in the modelling process. To address this, those areas where the A-SSj-PTC value was less than 0.75 were discarded. In addition, synchrony values were not available for one remaining location in both 2002 and 2003 and so these were discarded also. This resulted in 25 locations in 2002 and 28 locations in 2003 being available for the modelling process.

### 5.5.2 Results

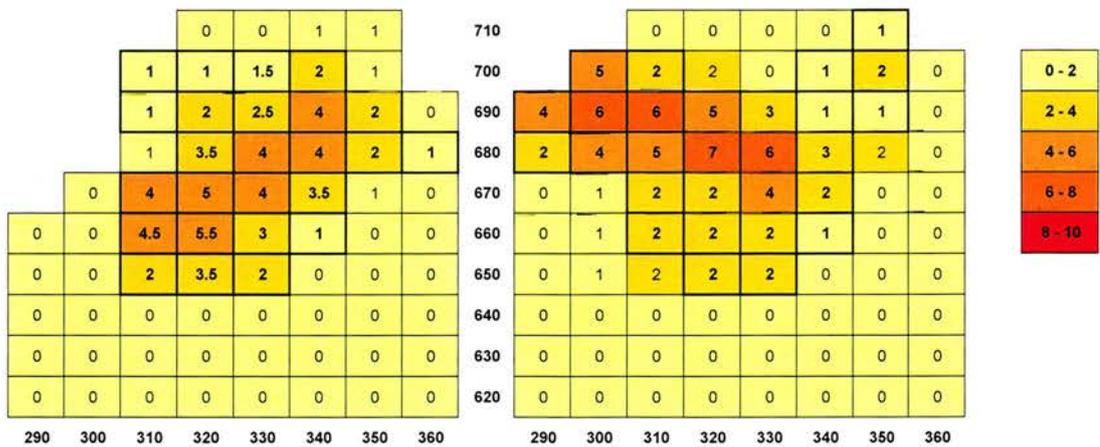
Geographical distributions of synchrony, aggressive interaction and median density values for 2002 and 2003 are shown in Figure 5.5.2.1. Topography values are shown in Figure 5.5.2.2. From these it can be seen that median density tends to be greater in areas of low cost distance to pools. Median elevation and slope tend to increase with cost distance to sea indicating the



(a) Female reproductive synchrony



(b) Rates of female aggression



(c) Median female density

Figure 5.5.2.1. Distributions of reproductive synchrony, female aggression and median density in 2002 and 2003.

Axes represents OSGB eastings (prefix 181\*\*\* and northings (prefix 1032\*\*\*). Map units are in metres.

Bold locations are those included in model.

(b) Rates of female aggression calculated within grid cells in 2002 and at 10m radii around grid cell centres in 2003.

All other calculations at 10m radii around grid cell centres.

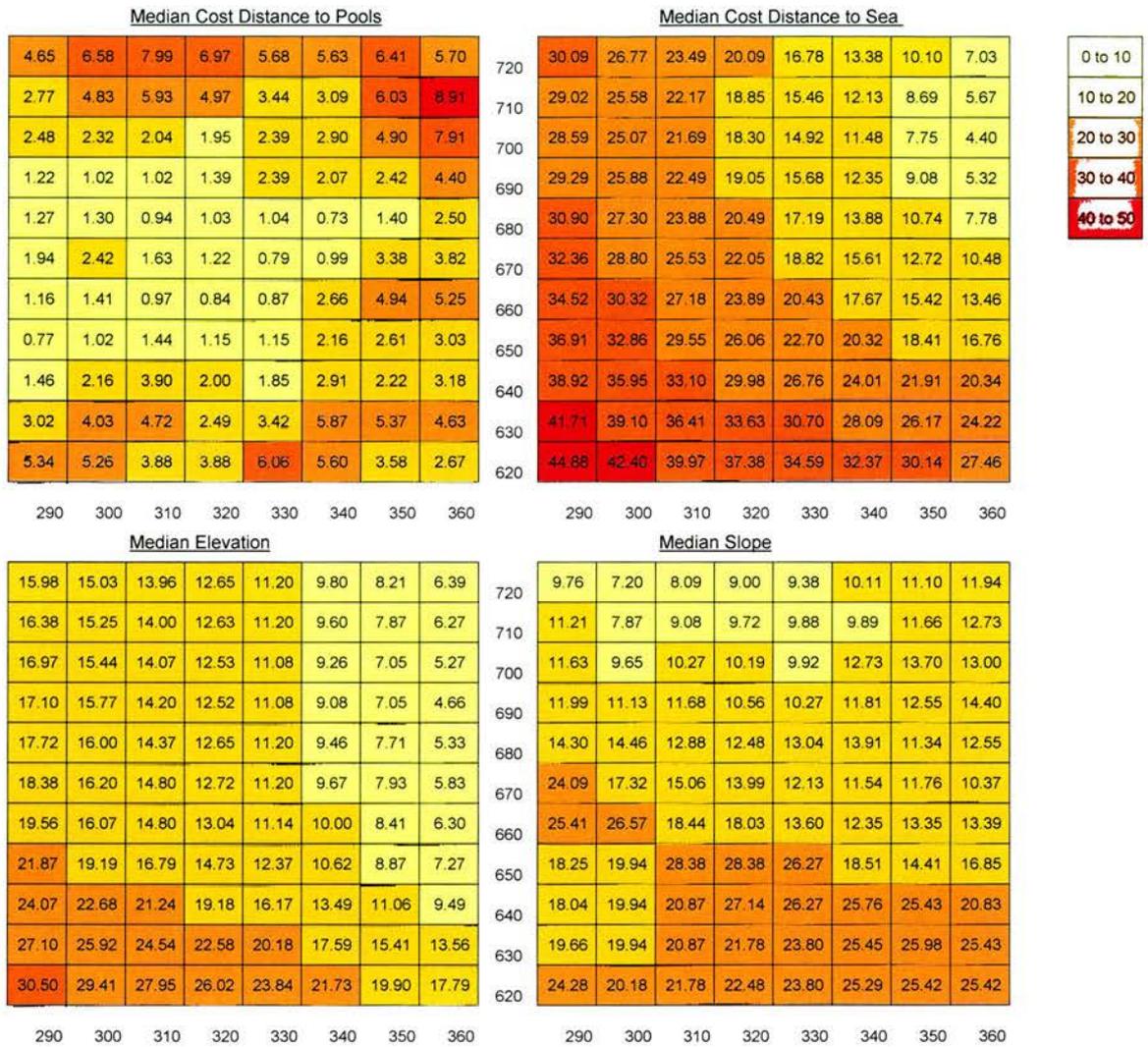


Figure 5.5.2.2. Distributions of median cost distance to pools, cost distance to sea, elevation and slope in the study area. Axes represents OSGB eastings (prefix 181\*\*\*) and northings (prefix 1032\*\*\*). Map units are in metres.

position of the access gully at north-east corner of the study area and incline of the hill from north-east to south-west.

In 2002 all variables displayed spatial autocorrelation (Moran's I >2.32,  $p < 0.05$ ) at a 10m scale apart from aggressive interactions (Moran's I = 1.33,  $p > 0.05$ ) (Table 5.5.2.1). This is possibly due to inconsistency in the way that aggression data was sampled. In 2003 all variables were spatially autocorrelated (Moran's I >3.57,  $p < 0.05$ ) apart from A-SSj (Moran's I=1.89,  $p > 0.05$ ) and reproductive synchrony (Moran's I = -0.07,  $p > 0.05$ ).

Table 5.5.2.1 Spatial autocorrelation statistics of multivariate input data from 2002 and 2003.

<u>2002 Season</u>			<u>2003 Season</u>		
Variable	Moran's I	p	Variable	Moran's I	p
Median ASSj (response)	3.464	< 0.05	Median ASSj (response)	1.893	0.06
Synchrony	2.317	< 0.05	Synchrony	-0.066	0.95
Aggression	1.333	0.18	Aggression	3.567	< 0.05
Distance to pool	3.111	< 0.05	Distance to pool	5.409	< 0.05
Distance to sea	5.419	< 0.05	Distance to sea	6.075	< 0.05
Elevation	5.027	< 0.05	Elevation	6.011	< 0.05
Slope	4.787	< 0.05	Slope	4.824	< 0.05
Median density	3.226	< 0.05	Median density	3.634	< 0.05

The minimal non-spatial linear model describing A-SSj values in 2002 retained synchrony, distance to pool and median density as significant covariates (covariates:  $p < 0.05$ , model:  $F(3,21)=19.91$ ,  $p < 0.05$ ) (Table 5.5.2.2(a)). However, spatial autocorrelation is evident in the residuals of this model fit (Moran's I =1.69,  $p < 0.05$ ). The minimal non-spatial linear model for 2003 retained distance to pool, distance to sea, elevation and median density as significant covariates (covariates:  $p < 0.05$ , model:  $F(4,23)=6.22$ ,  $p < 0.05$ ) (Table 5.5.2.2(b)). As maybe expected by the lack of spatial autocorrelation in the response variable, the

Table 5.5.2.2. Multivariate model outputs explaining A-SSj in 2002 and 2003.  
See text for details. \* actual p = 2.388e-6. \*\* actual p = 0.04575

(a) 2002 Season non-spatial minimal linear model

Variable	Coefficient	Std. Error	t	p
Intercept	0.550	0.140	3.914	< 0.05
Synchrony	-0.875	0.174	-5.028	< 0.05
Distance to pool	0.094	0.024	3.882	< 0.05
Median density	0.102	0.016	6.193	< 0.05
AIC = -114.33    Adjusted R2 = 0.70    F(3,21) = 19.91				* < 0.05
Moran's I on residuals at lag distance of 10m = 1.6875				** < 0.05

(b) 2003 Season non-spatial minimal linear model

Variable	Coefficient	Std. Error	t	p
Intercept	0.474	0.101	4.656	< 0.05
Distance to pool	0.081	0.021	3.915	< 0.05
Distance to sea	0.071	0.015	4.867	< 0.05
Elevation	-0.138	0.030	-4.609	< 0.05
Median density	0.030	0.012	2.498	< 0.05
AIC = -134.94    Adjusted R2 = 0.44    F(4,23) = 6.22				< 0.05
Moran's I on residuals at lag distance of 10m = -0.7713				0.779

(c) 2002 Season lagrange multiplier test on minimal model at 10m lag

Specification	Statistic	df	p
LMerr	0.8805	1	0.348
LMlag	3.2859	1	0.070
RLMerr	0.5769	1	0.448
RLMlag	2.9824	1	0.084
SARMA (LMerr+RLMlag)	3.8629	2	0.145

(d) 2002 Season maximum likelihood spatial lag model

Variable	Coefficient	Std. Error	z	p
Intercept	0.382	0.148	2.578	< 0.05
Synchrony	-0.697	0.172	-4.065	< 0.05
Distance to pool	0.077	0.022	3.558	< 0.05
Median density	0.085	0.016	5.277	< 0.05
Rho	0.313	0.162	1.936	0.052
Wald statistic = 3.7473				0.053
LM test for residual autocorrelation = 0.0596				0.807

(e) 2002 Season non-spatial linear model with distance to sea and elevation included

Variable	Coefficient	Std. Error	t	p
Intercept	0.703	0.178	3.946	< 0.05
Synchrony	-0.845	0.173	-4.890	< 0.05
Distance to pool	0.092	0.028	3.279	< 0.05
Distance to sea	0.017	0.013	1.249	0.227
Elevation	-0.041	0.027	-1.511	0.147
Median density	0.098	0.017	5.902	< 0.05
AIC = -113.71    Adjusted R2 = 0.71    F(5,19) = 12.93				< 0.05
Moran's I on residuals at lag distance of 10m = 1.3278				0.092

residuals of this model were not spatially autocorrelated (Moran's I = -0.77,  $p > 0.05$ ).

Although not significant, the Lagrange multiplier test suggests the inclusion of a spatially lagged weighting of the response variable is the most appropriate alternative model specification for the 2002 data (LMlag = 3.29,  $p = 0.07$ , RLMlag = 2.98,  $p = 0.08$ ) (Table 5.5.2.2(c)). Under the spatial lag specification the synchrony, distance to pool and median density covariates were still significant ( $p < 0.05$ ) but the spatial component, rho, was not ( $p > 0.05$ ) (Table 5.5.2.2(d)). The model itself was not significant (Wald t = 3.75,  $p > 0.05$ ), but spatial structure had been addressed as no residual spatial autocorrelation was present (LM test = 0.06,  $p > 0.05$ ). This provides a slight dilemma. On one hand, the spatial lag model adequately addresses the problem of spatial autocorrelation, but does not provide a significant fit. On the other hand, the non-spatial linear model provides a good fit but suffers from residual spatial autocorrelation. There were two extra covariates included in the minimal model for 2003 that were not included for 2002. These were cost distance to sea and elevation. It is possible that the spatial structure incorporated within these two variables explained enough spatial structure to result in no residual spatial autocorrelation for the 2003 model. These variables were forced into an alternative non-spatial model for 2002. The resultant model provided a significant fit ( $F(5,19) = 12.93$ ,  $p < 0.05$ ) although the two extra variables themselves were not significant (Table 5.5.2.2(e)). Most notably spatial autocorrelation was absent from the residuals. It is also worth noting that the original non-spatial minimal model for 2002 was highly significant ( $p = 2.4 \times 10^{-6}$ ), whereas the Moran's I test on the residuals of this model was only marginally significant ( $p = 0.046$ ). Given that the result of

spatial autocorrelation is possible rejection of the null hypothesis when it is true, the presence of a very high significance value suggests that even if spatial autocorrelation was present, the model conclusions may still be valid. In addition, covariate significance was equal for the spatial lag model, the non-spatial linear model, and the model incorporating spatial structure through the addition of extra variables. It is probably reasonable to conclude, then, that the three original variables of synchrony, distance to pool and median density were significant predictors of A-SSj in 2002 and that distance to pool, median density, distance to sea and distance to access were significant predictors of A-SSj in 2003.

### 5.5.3 Discussion

This analysis has made explicit three primary predictors of area based social stability: reproductive synchrony, cost distance to pools and median density. Elevation and cost distance to sea may also be important. Interestingly, there seems to be no obvious relationship between levels of aggression and social stability. It was originally hypothesised that aggression reduction and social stability may co-vary for two reasons. Firstly a reduction in aggression may reduce the stimulus for individuals to change location, and therefore neighbours. Secondly, aggression reduction through familiarity (Johnsson, 1997; Utne-Palm & Hart, 2000) was hypothesised to be a possible adaptive benefit of social stability. It was thought that lower levels of aggression in areas of greater social stability would provide a real-time advantage to mothers while nursing a pup, as the chance of injury and failure of the mother-pup bond may be reduced (Anderson et al., 1979). The distribution of levels of aggression does not relate

to that of social stability. Levels of aggression were very low on the colony, and perhaps lower than those on other colonies (Redman, 2002). It is possible that levels were so low that the sample size did not allow for accurate description of the variance in aggression, with too much weight being placed on individual observations. It is also possible that the resolution of behavioural observations was insufficient to describe behavioural activity. If the sampling protocol was mismatched to the behaviours under study (as is possible for aggression data from 2002) then an inaccurate representation of behaviours will be recorded. It is possible that this was also the case for aggression data from 2003. The area under continuous observation in 2003 was 7600m<sup>2</sup> and it is possible that not all interactions that took place were recorded. The eye may have been drawn to certain interactions, perhaps closer to the observer or of higher intensity, to the disregard of others. In addition, behavioural observations were only carried out during a restricted number of afternoons. Although unlikely it is possible that aggressive interactions occurred more often at times other than those observed. It is also possible that the level of disruption under study was miss-targeted. Lower levels of stress than those inciting interactions may vary with social stability. An indicator of such might be alert responses. However, due to a lack of confidence in the observer's ability to record all alert responses accurately over such a large study area, these behaviours were not analysed. Physiological measures such as heart rate may be useful as alternative indicators of psychological stress (deJong et al., 2000; Hopster & Blokhuis, 1994).

Reproductive synchrony was a significant covariate in the 2002 model, but in a direction that might at first seem unintuitive. As reproductive synchrony increased, social stability decreased. A possible explanation for this is that a

group of animals at similar stages in lactation may be more fractious than a group in which timing is staggered. For instance, mothers appear to be more aggressive, and so perhaps less settled, towards the start of lactation (Boness et al., 1982; Redman, 2002). Synchrony of early lactation stages may therefore make groups less stable through increased likelihood of displacement. On the other hand, if a new arrival joins the vicinity of a mother that is already well established, the two may be less likely to impinge on one another. One might have expected that an increase in synchrony would drive an increase in social stability as mothers enter and leave an area at similar times. However, an indication that this is not the case suggests that short-term behavioural activity is more influential to social stability than reproductive synchrony alone.

Social stability increased with density in both years. This is evident from the maps of social stability and animal locations (Figures 5.3.1.1 and 5.3.1.2) where social stability is greater towards the centre of main aggregations. Animals tend to aggregate around resources such as fresh water pools so it would be expected that social stability would increase as access to pools increases (Twiss et al., 2000; Twiss et al., 2001). However, the reverse is true. This suggests that social stability is not greatest within the pool itself (a resource that will be shared by many individuals) but perhaps at a moderate distance from them. Social stability also appears to increase with cost distance to sea, but decrease with elevation. As the distribution of these two variables are similar (see Figure 5.5.2.2) it is likely that they are moderating each other in the model to explain increased social stability towards central areas of the study area. Social stability therefore seems greatest in areas towards the centre of the colony,

with moderate access to pools and that are well populated by animals at different stages of lactation.

5.6 The effect of individual-based social stability (I-SSj) and other factors on reproductive performance

5.6.1 Methods

Reproductive performance estimates were available for a sub-sample of the individuals present in 2002 and 2003. Pup mass at birth and pup growth rate are related to maternal size (Pomeroy et al., 1999). Therefore, an unbiased estimate of maternal efficiency is best used to describe the relative ability of a grey seal mother to realise her body stores as an increase in the body condition of her pup, a good predictor of first year survival (Hall et al., 2001). Maternal efficiency is calculated as pup daily growth rate divided by maternal daily mass loss rate. Data from 2002 and 2003 were examined both independently using simple linear models and together using linear mixed-effects models with the 'nlme' package in R (Pinheiro et al., 2004; R Development Core Team, 2004). Performance data was available for some animals in both 2002 and 2003 and so some data points lack independence due to repeated measures from the same individual. Mixed-effects models account for this by grouping non-independent data points and allowing different intercept terms for each group. Random intercept values are taken from a normal distribution around a population mean. These are termed random effects as they relate to a random sample of the population under study and allow assessment of the variation between groups. Covariates included in the model are termed fixed effects as they provide the regression slope common (and so 'fixed') to all groups (Pinheiro & Bates, 2000). Here, the grouping random effect is seal identity and the fixed effects are one of I-SSj, year, pupping date, cost distance to the sea, elevation, slope, reproductive synchrony or cost distance to pools. Multivariate analysis was not possible

because of the small sample size. While I-SSj was calculated around each individual, the variables cost distance to sea, elevation, slope, reproductive synchrony and cost distance to pools were only available as median values around grid cell centres. The value for these variables was therefore taken as that around the grid cell centre closest to the centroid position for each individual.

### 5.6.2 Results

Table 5.6.2.1. shows the raw data from 2002 and 2003 for the 12 animals for which maternal efficiency measures were available. Maternal efficiency values were available for five of these individuals (animals 1,2,3,5 and 6) in both 2002 and 2003 giving a total of 17 data points. Four of these were discounted as outliers. Seal 6 in 2002 lost her pup and so had a maternal efficiency value of zero. The constraints that an animal which is not rearing a pup is under may be different to those for animals that are and so she was dropped from the analysis. It is interesting to note that she returned in 2003 and successfully reared a pup with a relatively high maternal efficiency value. Seal 7 in 2002 and seals 11 and 12 in 2003 were also dropped from the analysis due to having low I-SSj-PTC values.

**Table 5.6.2.1** I-SSj and maternal efficiency values from 2002 and 2003. \**Italics* denote outliers. Significance denotes deviation from null model at  $\alpha=0.05$ .

Seal.no	Seal	Year	Maternal Efficiency	I-SSj	I-SSj.PTC	Significance
1	65	2002	0.19	0.13	1.00	x
1	113	2003	0.45	0.52	1.00	x
2	81	2002	0.40	0.09	1.00	↓
2	69	2003	0.57	0.69	1.00	↑
3	32	2002	0.54	0.48	1.00	x
3	46	2003	0.50	0.23	1.00	x
4	19	2002	0.55	0.53	1.00	↑
5	44	2002	0.57	0.45	1.00	x
5	15	2003	0.62	0.33	1.00	x
6	31	2002	0.00*	0.29	1.00	x
6	18	2003	0.63	0.38	1.00	x
7	78	2002	0.51	0.00	0.17*	↓
8	108	2003	0.58	0.20	0.90	x
9	78	2003	0.63	0.48	1.00	x
10	40	2003	0.69	0.30	1.00	x
11	109	2003	0.44	0.39	0.43*	x
12	115	2003	0.59	0.00	0.29*	x

None of the available explanatory variables were statistically significant predictors of maternal efficiency in either simple linear models for each year or linear mixed effects models for both years (Table 5.6.2.2). However, I-SSj proved the most likely candidate for showing at least a trend in relation to performance values. Multivariate analysis was not possible as this produced problems with normality of residuals, due most likely to the small sample size involved. Only the effect of I-SSj on performance will be considered further.

When the data from 2002 is observed in isolation there appears to be a trend of increased maternal efficiency with increased I-SSj ( $n=5$ ,  $F(1,3)=7.00$ ,  $p=0.077$ ,  $\text{Adj.R}^2=0.60$ )(Figure 5.6.2.1.). This is not repeated in 2003 ( $n=8$ ,  $F(1,6)=0.186$ ,  $p=0.681$ ,  $\text{Adj.}^2=-0.13$ ) where there is no significant trend of I-SSj on maternal efficiency (Figure 5.6.2.2.). Figure 5.6.2.3. shows the data from both years plotted together. In this figure an upward triangle represents an

**Table 5.6.2.2.** Simple linear and linear mixed effects models explaining maternal efficiency in 2002 and 2003. See text for discussion.

2002 data		Variables:				Model:			
Model		Coeff.	Std.Error	t	p	Adj.R2	(DF) F	p	
1	Intercept	0.234	0.093	2.513	= 0.087	0.60	(1,3) 7.00	= 0.077	
	I-SSj	0.642	0.243	2.646	= 0.077				
2	Intercept	1.121	0.274	4.083	< 0.05	0.56	(1,3) 6.15	= 0.089	
	Pupdate	-0.017	0.007	-2.481	= 0.089				
3	Intercept	0.079	0.231	0.340	= 0.756	0.31	(1,3) 2.76	= 0.195	
	Sea	0.018	0.011	1.663	= 0.195				
4	Intercept	-0.151	0.385	-0.392	= 0.721	0.27	(1,3) 2.50	= 0.212	
	Elevation	0.047	0.030	1.581	= 0.212				
5	Intercept	0.018	0.301	0.059	= 0.957	0.22	(1,3) 2.16	= 0.238	
	Slope	0.029	0.020	1.469	= 0.238				
6	Intercept	0.485	0.170	2.854	= 0.065	-0.31	(1,3) 0.06	= 0.829	
	Pools	-0.023	0.098	-0.235	= 0.829				
7	Intercept	0.433	0.179	2.414	= 0.095	-0.33	(1,3) 0.01	= 0.921	
	Synchrony	0.092	0.856	0.108	= 0.921				

2003 data		Variables:				Model:			
Model		Coeff.	Std.Error	t	p	Adj.R2	(DF) F	p	
1	Intercept	0.616	0.080	7.721	< 0.05	-0.13	(1,6) 0.19	= 0.681	
	I-SSj	-0.082	0.190	-0.432	= 0.681				
2	Intercept	0.730	0.160	4.563	< 0.05	-0.02	(1,6) 0.86	= 0.389	
	Pupdate	-0.004	0.004	-0.929	= 0.389				
3	Intercept	0.641	0.102	6.264	< 0.05	-0.10	(1,6) 0.34	= 0.579	
	Sea	-0.003	0.005	-0.587	= 0.579				
4	Intercept	0.677	0.128	5.304	< 0.05	-0.07	(1,6) 0.56	= 0.484	
	Elevation	-0.007	0.010	-0.747	= 0.483				
5	Intercept	0.487	0.171	2.839	< 0.05	-0.11	(1,6) 0.33	= 0.588	
	Slope	0.008	0.013	0.573	= 0.588				
6	Intercept	0.655	0.082	7.987	< 0.05	-0.02	(1,6) 0.85	= 0.393	
	Pools	-0.340	0.370	-0.920	= 0.393				
7	Intercept	0.589	0.047	12.402	< 0.05	-0.16	(1,6) 0.02	= 0.892	
	Synchrony	-0.003	0.023	-0.141	= 0.892				

2002 and 2003 data								
Model	Random	St. Dev	Fixed	Coeff.	DF	t	p	Model AIC
1	Intercept	0.094	Intercept	0.426	8	7.525	< 0.05	-15.48
	Residual	0.058	I-SSj	0.335	3	3.002	= 0.058	
2	Intercept	0.072	Intercept	0.467	8	9.782	< 0.05	-15.21
	Residual	0.074	Year	0.122	3	2.405	= 0.096	
3	Intercept	0.040	Intercept	0.933	8	5.361	< 0.05	-14.98
	Residual	0.092	Pupdate	-0.011	3	-2.315	= 0.104	
4	Intercept	0.080	Intercept	0.417	8	3.008	< 0.05	-10.90
	Residual	0.091	Sea	0.006	3	0.964	= 0.406	
5	Intercept	0.080	Intercept	0.400	8	2.177	= 0.061	-10.60
	Residual	0.092	Elevation	0.011	3	0.806	= 0.479	
6	Intercept	0.064	Intercept	0.444	8	2.513	< 0.05	-10.33
	Residual	0.103	Slope	0.007	3	0.559	= 0.615	
7	Intercept	0.076	Intercept	0.513	8	5.455	< 0.05	-10.09
	Residual	0.097	Synchrony	0.152	3	0.357	= 0.745	
8	Intercept	0.071	Intercept	0.537	8	7.937	< 0.05	-9.98
	Residual	0.101	Pools	0.003	3	0.095	= 0.930	

**2002 Maternal Efficiency and I-SSj**

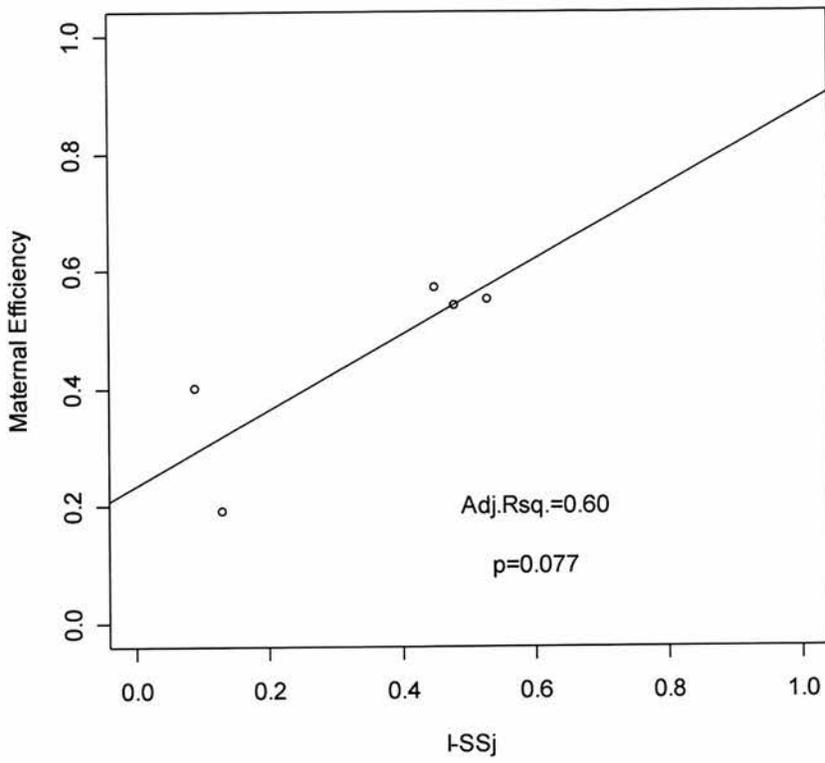


Figure 5.6.2.1. I-SSj and maternal efficiency in 2002.

**2003 Maternal Efficiency and I-SSj**

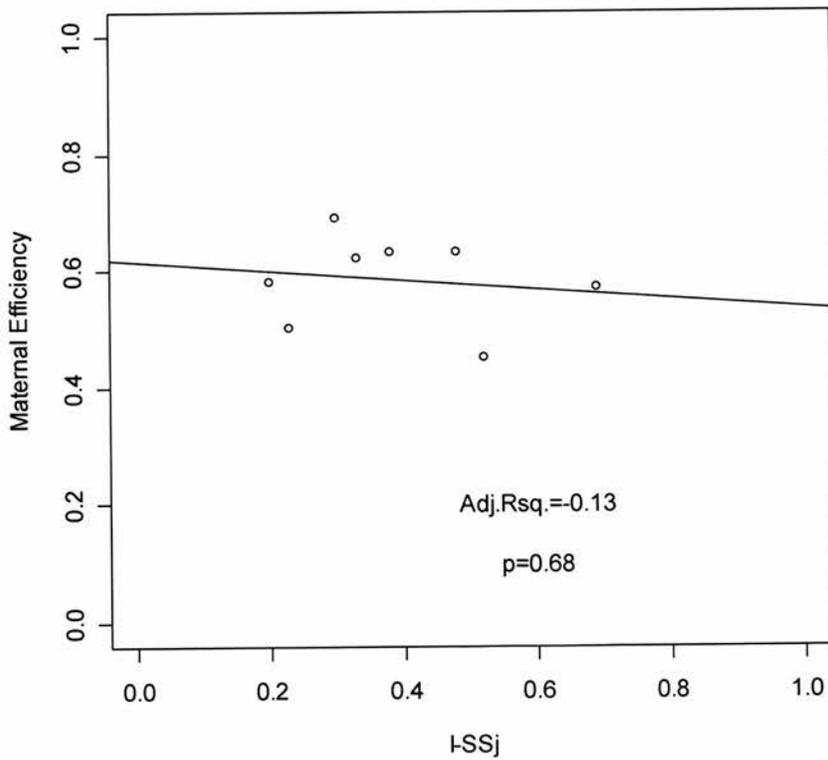


Figure 5.6.2.2. I-SSj and maternal efficiency in 2003.

**Maternal Efficiency and I-SSj in 2002 and 2003**

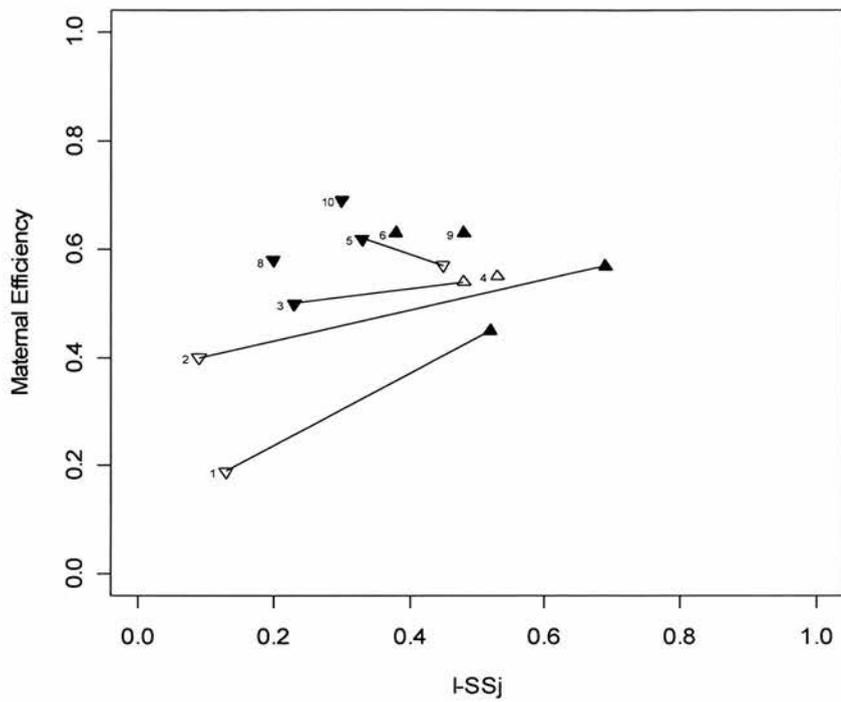


Figure 5.6.2.3. I-SSj and maternal efficiency in 2002 and 2003. See text for details.

**Mixed-Effects Model Output**

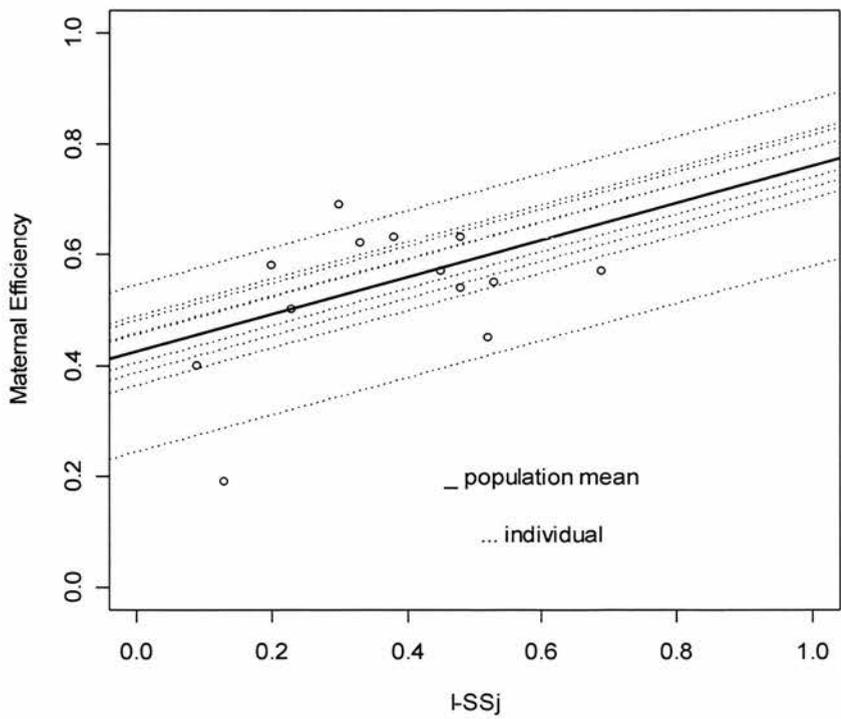


Figure 5.6.2.4. I-SSj and maternal efficiency in 2002 and 2003: mixed-effects model output. See text for details.

observation of I-SSj that was greater than simulated and a downward triangle represents an observation of I-SSj that was lower than simulated. Open triangles denote data from 2002, closed triangles from 2003 and repeated measures from the same individuals are joined by lines. Three of the four individuals for which repeated measures were available showed increased maternal efficiency with increased I-SSj. In addition for these three, when social stability (and maternal efficiency) was low it was lower than simulated values, and when it was high it was higher than simulated values. This is most noteworthy for animal 2 whose I-SSj value was significantly lower than expected from simulation in 2002 and significantly higher than expected from simulation in 2003 (at  $\alpha = 0.05$ ) (Table 5.4.2.1.). Animal 5, however, experienced lower maternal efficiency with higher I-SSj values, both of which were lower than simulated. The results of the mixed-effects model can be seen in Figure 5.6.2.4. The bold line illustrates the population mean with an intercept value of 0.426 and a standard deviation of 0.094 (DF=8,  $t=7.53$ ,  $p<0.05$ ). The dotted lines represent those for each individual, taken from a normal distribution around the population mean. This illustrates the variability between seals. The residual standard deviation is 0.058 and this represents the variability within seals. The common slope to all lines has a value of 0.334 and this represents the effect, although not significant, of I-SSj on maternal efficiency values (DF=3,  $t=3.00$ ,  $p=0.0576$ ). The AIC for the model was -15.48. Of all the available parameters, I-SSj appears to be the best fitting, although not significant, covariate to reproductive performance. Reproductive performance tends to increase with I-SSj suggesting that social stability may have an adaptive benefit on the North Rona colony.

### 5.6.3 Discussion

In a previous model describing factors affecting pup mass at weaning on the North Rona colony 75% of the variation explained was due to unknown effects characterised within each individual (Pomeroy et al., 1999). Maternal post-partum mass, duration of lactation, maternal length and year explained the majority of the remaining variation. This study shows that social stability has the potential to explain some of that unknown variation. There is a non-significant but intriguing trend for increased maternal efficiency with increased I-SSj in both single year linear and two year linear mixed-effects models. A complication to these models, however, is that data points may suffer bias due to the temporal regime under which they were collected (Chapter 5.2). For this reason, the most compelling evidence is that three out of four individuals enjoyed high values of maternal efficiency when experiencing higher I-SSj than would be expected by chance, and suffered from lower maternal efficiency when experiencing lower I-SSj than would be expected by chance. In addition, for one of these animals both the high and low I-SSj values were significantly different to those expected from the simulation.

This analysis is hindered by the limited sample size, making further investigation difficult. It is possible that an increase in sample size would allow verification or rebuttal of this marginally insignificant trend. Substantial differences in I-SSj and maternal efficiency occur between individuals. It would therefore be most revealing to gather more longitudinal data to aid in assessment of how animals respond to different I-SSj values between years. In addition, it is possible that maternal efficiency and social stability may have a non-linear or

threshold relationship such that very low values are detrimental, but moderate or high values are similar in effect.

There are implications of social effects on maternal performance not only for immediate site and neighbour choice by a mother but also for colony-wide success where the potential exists. Levels of aggression appear lower on North Rona than on another Scottish colony on the Isle of May (Redman, 2002). While the North Rona colony is characterised by inland locations and little travel to the sea during lactation, animals on the Isle of May are situated mainly in tidal gullies and commute to the sea often (Anderson et al., 1975; Redman et al., 2001; Twiss et al., 2000). It would seem that the colony on the Isle of May with higher movement and levels of aggression may therefore be less disposed to an environment of high social stability and so possibly at a disadvantage in reproductive performance. However, there is no evidence for this as while the colony on North Rona is stable or declining, the colony on the Isle of May has recently gone through a period of substantial population growth [Hiby, 1996 #79; Pomeroy, 2000 #80; Pomeroy, pers. comm.].

### 5.7 General Discussion

This study has demonstrated a variance in social stability across the grey seal breeding colony on North Rona, Scotland. In addition, this variance is reflected in the range of social stability values that individual mothers experience. Breeding grey seal females on this colony must therefore not only contend with heterogeneity in the physical environment (see Pomeroy et al., 2000; Twiss et al., 2001; Twiss et al., 2000) but also with complexity in the social landscape. Although methods for quantification of association between individuals are well established (for example: Chilvers & Corkeron, 2002; Myers, 1983; Underwood, 1981; Wilkinson, 1985), these are mostly inappropriate for use on breeding pinnipeds (Whitehead & Dufault, 1999). As such, a method for describing this social landscape has been conspicuously lacking from the biologists' toolbox. This is the first time, to the author's knowledge, that such a detailed quantification of sociality has been undertaken within a pinniped breeding rookery.

As this quantification of social stability is a novel method for describing the social environment it is hard to compare these findings to other systems. Social stability can be inferred from studies based on pair-wise association indices. Groups characterised by very high association scores between individuals are likely to be socially stable and groups characterised by predominantly low association scores between individuals are likely to be unstable. Lazo (1994) used this principal to show that feral cattle (*Bos Taurus*) formed stable social groupings between which there was little (but some) mixing. Alternatively, Lott and Minta (1983) found that groupings of American Bison (*Bison bison*) were unstable, association scores being generally low. Most

notably, Pomeroy et al. (2005) found that grey seal mothers on North Rona showed evidence of pair-wise associations between years, suggesting the possibility of active social behaviour within this colony (although see Chapter 6). Until now, however, nothing was known about the social environment that mothers experience within a single breeding season.

Although robust to the levels of missing data experienced in this study the method is perhaps weakest in ability to deal with inconsistency in the temporal regime over which data is gathered. All measures that are punctuated by time intervals will suffer from this problem to a certain extent. For instance, it is likely that for pair-wise measures, as is evident here, an increase in time interval is likely to be associated with a decrease in the probability of associations being maintained (Whitehead & Dufault, 1999; Whitehead et al., 1991).

The effect of temporal inconsistency is not important when comparing observed values to those from simulation. This is because the temporal structure within the simulation was identical to that observed. Any artefactual effect of time on social stability values will therefore be equally influential for expected as for observed values. This is not the case when comparing social stability values either between individuals or areas that have been calculated over different temporal regimes. If such comparisons are to be made then the most conclusive results will come from comparing only values as high or low with reference to significant deviation from the null model.

There were both areas and individuals of significantly greater and lesser social stability than would be expected by chance. One area of the colony was associated with significantly elevated social stability in both years. This suggests that social stability can be consistently related to particular areas over successive

seasons. Experienced mothers may therefore be at an advantage in knowing where these areas are and this in turn may have a positive feedback to site fidelity (Pomeroy et al., 1994). There was also an area that was significantly lower in social stability than would be expected by chance. This may be an area to avoid. In turn, individuals are able to experience significantly elevated and reduced social stability to the null models predictions. Individuals therefore appear able to influence the social environment in which they raise a pup. It would be interesting to investigate whether the social stability experienced by an individual affects its choice of pupping sites in subsequent years. However, there is no evidence that pupping failure affects site fidelity (Pomeroy et al., 1994).

Topography is known to affect breeding behaviour in grey seals. Females preferentially locate in areas with good access to water where they are able to spend more time interacting with their pups and less time in locomotion and associated aggressive interactions (Twiss et al., 2000). Such areas, towards the centre of the colony and with moderate access to pools on North Rona are also associated with elevated levels of social stability. Topographic parameters may therefore provide an important pressure on social stability as areas of high topographic quality predispose individuals to more placid and sedentary behaviours.

Social stability is unlikely to be of importance if it has no associated benefit. However, it is clear that the day-to-day environment that an animal experiences has the potential to profoundly influence its own behaviour and so have repercussions for reproductive success. Social factors have been shown to affect reproductive success in a variety of systems. For instance while sea lions (*Otaria byronia*) benefit from increased pup survival in colonies rather than

solitary pairs, elephant seal (*Mirounga leonina*) pups survive better in low density breeding conditions (Baldi et al., 1996; Campagna et al., 1992). This appears to be mainly due to harassment by the large males of these sexually dimorphic species and it is likely that moderate densities where male harassment is moderated would be more beneficial than extremely high or low densities. Although grey seals are sexually dimorphic males are not hugely bigger than females and females appear quite able to reverse unwanted male approaches (Anderson et al., 1975; pers. obs.). However, on Sable Island, Nova Scotia, grey seal females that pupped late in the season, at a time when male disturbance was high, demonstrated reduced maternal performance (Boness et al., 1995). In a review of dominance and reproductive success in non-human animals, Ellis (1995) concluded that for females, studies were split between rank and success being positively correlated and there being no relationship between the two. Dominance relationships are difficult to evaluate between female grey seals as interactions rates are low and initiators, recipients and outcomes of interactions are often difficult to identify.

In this study it was found that maternal performance during lactation tended to be greater for individuals that experienced elevated levels of social stability. In humans, stress related psychosocial factors such as social instability, lack of participation and support have been shown to increase the risk of giving birth to small for gestational age infants (Dejin-Karlsson et al., 2000). Whether psychosocial factors such as this could influence maternal performance in grey seals or whether any benefit of social stability would accrue through factors such as a changes in time budgets and reduction in aggressive interactions is unknown.

Other than forming temporary aggregations, most likely as a predator defence mechanism against terrestrial predators (Macdonald, 1983) and in response to resource availability, breeding grey seals do not appear to be highly social. However, if the social stability experienced by a mother can affect maternal efficiency then it becomes a very important factor in the life history of this species and perhaps a driving force behind further social development. This provides insight into how sociality can not just be promoted and persist as an adaptive benefit to grey seals but how sociality can be and may have been promoted across the animal kingdom. In addition, if social stability is itself driven, at least in part, by topographic factors then this in turn provides a demonstration of the importance of environmental conditions on the possibilities for social evolution.

# **Chapter 6**

## **Between year sociality**

## 6.1 Introduction

Sociality has predominantly been investigated in animals that can be observed consistently or repeatedly over prolonged periods of time (Chilvers & Corkeron, 2002; Coakes & Whitehead, 2004; Connor et al., 2000; Lott & Minta, 1983; Underwood, 1981; Wilkinson, 1985). For instance, in fission-fusion societies pair-wise associations are often quantified by assessing the proportion of time that individuals are observed together, proximity in time and space being a prerequisite to, and so used as a proxy for, behavioural interaction (Whitehead & Dufault, 1999). In Chapter 5 of this thesis social stability within the breeding colony of grey seals on North Rona was investigated during two breeding seasons. Here, sociality was quantified as the change in identities associated with areas or individuals throughout each breeding period. Each individual, however, only remains on the colony for around 3 weeks and the breeding season itself spans only around 2 to 3 months (Anderson et al., 1975). After this time, animals disperse from the colony and do not return *en mass* until the breeding season one year later, when they become available again for observation. Long-term associations between grey seal females can currently only be quantified between these temporary breeding aggregations. If active sociality occurs within breeding seasons (see Chapter 5) then it is also possible that active sociality occurs between breeding seasons. In this chapter I investigate whether mothers breeding on North Rona choose to breed with others that they have been associated with in a previous breeding attempt.

Association can be defined for grey seal mothers as positive for those whose residence on the colony is separated by less than a certain spatial and temporal threshold. The spatial scale of association used here is 20m (see

Chapter 3, (Redman, 2002)). As the average length of lactation for an individual mother is 18 days (Pomeroy et al., 1999), using a temporal scale of 9 days ensures that animals are within the spatial threshold for at least half of their residence.

It is possible to measure sociality across breeding attempts in two ways. Firstly, the maintenance of specific pair-wise associations can be assessed across breeding attempts. As not all individuals' associates need be known in order to assess specific pair-wise associations this can be carried out for a sub-sample of the population. However, in doing so one only learns about a small part of the social processes being played out. That is, little information is gained of the wider social environment that animals experience. In assessing the maintenance of only some pair-wise associations, then, the maintenance, loss and gain of all other associations are ignored. The second method is to measure the social stability (I-SSj) that individuals experience across breeding attempts (see Chapter 4). In order to do so all of an individual's associates must be known in both years. Sub-sampling for I-SSj within a population would therefore be highly inefficient and it is better to assess the whole of a smaller population. The primary benefit of I-SSj is that it constitutes a composite measure of the maintenance of associations, the loss of old associations and the gain of new associations and as such provides a much fuller picture of an individual's sociality.

Grey seal mothers on North Rona have been shown to be highly spatially and temporally faithful to previous breeding events (Pomeroy et al., 1994; Redman, 2002). Clearly, if mothers return to exactly the same place at exactly the same time every year they would re-associate with exactly the same

individuals. However, site fidelity is estimated to be around 30-40m for these animals and temporal fidelity is within a couple of days (Pomeroy et al., 1999; Redman, 2002). As associations here are defined within a range of 20m, then, it is likely that, unless movement is precisely coordinated, there will be a change in animals' associates between years. It may also be expected that animals who only change their location by a small distance may have a higher chance of re-associating with previous associates than animals that change location by a large distance.

Hypotheses regarding animal behaviour are difficult to test in the wild because it is not usually possible to isolate any single part of an animal's behavioural repertoire. However, given knowledge of the primary non-social influences on behaviour, simulation, or constrained randomisation, can be used to realistically estimate behaviour in the absence of sociality (Whitehead, 1999; Bejder et al., 1998). Simulations were constructed here to quantify the expectations of re-association and social stability given known inter-annual distributions of site fidelity, temporal fidelity and site preference. From these it was possible to test the observed rates of re-associations and social stability values for deviation from chance and so assess the possibility of active social coordination within the study population.

Section 6.2 of this Chapter describes the use of such a simulation to test observed occurrences of repeated pair-wise associations. These constitute a subsample of the larger population breeding on North Rona in the years 1998, 1999 and 2000 (see also Pomeroy et al., 2005b, Appendix B). In Section 6.3 the re-sighting rates of animals between 2002 and 2003 are evaluated to assess the apparent return rates of animals to the study area and influx and efflux to this

area from other parts of the North Rona colony. Section 6.4 is concerned with the description of social stability (I-SSJ) for all animals within the study area in 2002 and 2003. Observed social stability values were also tested against a null model to assess the possibility of active social organisation within the study population. In addition, environmental and behavioural influence on observed social stability values was assessed and the possible influence of social stability on maternal performance explored.

## 6.2 Pairwise associations

*This section describes the creation of the simulated null model of seal behaviour presented in Pomeroy et al. (2005) (Appendix B). The re-analysis and results from a revised data set are provided here. (A version of this data set was first presented in Redman's (2002) PhD thesis and the work presented here constitutes a thorough reworking and reanalysis of a revised version of this data set with entirely novel methodology)*

### 6.2.1 Quantification of pair-wise association

In Redman's thesis (2002) and the resultant paper by Pomeroy et al. (2005), pair-wise associations were quantified between 'known' individuals on the North Rona breeding colony during the 1998, 1999 and 2000 breeding seasons. 'Known' individuals were those for which pelage markings were recorded to enable subsequent recognition, and pupping site and date information was available. Although most attention was focused in predefined areas, known individuals were spread across the whole breadth of the Study Area (SA) on the North Rona breeding colony as defined in Pomeroy et al. (1994) and shown in Figure 2.1.1. (NB. the study area used elsewhere in this thesis is smaller than the SA presented here, approximating to roughly the eastern half of the SA).

### Defining associations

Known mothers were represented by a centroid location and birth date for each year in which they were present. Centroid locations were calculated as the centre of the 99% contour of a density map of all locations recorded for each

mother. These were computed using the POINTDENSITY command with 10m circular kernel estimators in ArcInfo Geographical Information System software (ESRI, Twiss, pers. comm.). Centroids therefore represent the centre of a mother's 'home range' whilst resident on the colony. Pair-wise associations within years were then quantified using the criteria of no more than 20m separation in centroid location and no more than 9 days difference in pupping date.

### Observed results

There were 58, 87 and 109 known mothers identified in 1998, 1999 and 2000 respectively. As the SA contains up to 500 individual mothers during any one season (Pomeroy, pers. comm.), this sample of known individuals represents around 10-20% of all the females in the SA.

A total of 132, 297 and 416 pair-wise associations were present between the known mothers in 1998, 1999 and 2000 respectively (Table 6.2.1.1). There were 30 known mothers common to 1998 and 1999. Between 29 of these there were 76 pair-wise associations in 1998, of which 8 were re-established in 1999 (Table 6.2.1.2). There were 44 known mothers common to 1999 and 2000. Between 32 of these there were 76 pair-wise associations in 1999, of which 7 were re-established in 2000 (Table 6.2.1.2). In total, therefore, out of 152 pair-wise associations present in the first of two years, 15 were re-established in the next.

Table 6.2.1.1 Within year pair-wise associations between known mothers in 1998, 1999 and 2000.

	1998	1999	2000
Number of known mothers	58	87	109
Number of known mothers involved in pairwise associations with each other	47	80	101
Number of pairwise associations between known mothers	132	297	416

Table 6.2.1.2 Between year pair-wise associations between known mothers in the periods 1998-1999 and 1999-2000

	1998-1999	1999-2000
Number of known mothers common to both years	30	44
Number of known mothers involved in association in year 1	29	32
Number of pairwise associations between known mothers in year 1	76	76
Number of known mothers involved in association in year 2	20	34
Number of pairwise associations between known mothers in year 2	19	58
Number of pairwise associations between known mothers common to both years	8	7

The frequency with which re-association occurred and the respective distances that each re-associating female moved between pupping attempts is shown in Table 6.2.1.3. For example, there were six occurrences in which a pair of mothers were observed to re-associate when one of that pair displayed a site fidelity distance of 0-10m and the other 10-20m. The joint probability of two mothers associated in year 1 both moving within a certain distance class and remaining associated in year 2 is summarised in Table 6.2.1.4. Probabilities

were calculated as the number of re-associations observed within a distance class divided by the number of associations in year 1 that would be theoretically possible in year 2 (as both of the mothers involved were present in both years). For example, 8 out of 152 associated mother pairs from the first year displayed site fidelity movements of over 10m *and* re-associated in the second year (probability = 0.053). It is important to note that this is not the probability that an associated mother pair would re-associate *given* site fidelity displacements of over 10m.

Table 6.2.1.3 Observed count of re-associations and pupping site displacements in consecutive years for known mothers in 1998, 1999 and 2000. See text for example.

Distance moved (m)		Female A								
		0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80+
Female B	0-10	.								
	10-20	6	.							
	20-30	1	1	.						
	30-40	.	.	1	.					
	40-50	.	.	.	.	.				
	50-60	.	.	.	.	2	.			
	60-70	.	.	.	.	1	1	.		
	70-80	.	.	.	.	.	.	.	.	
	80+	.	.	.	.	.	1	1	.	.

Table 6.2.1.4 Observed joint probability that mothers should move a certain distance and remain associated in consecutive years. See text for example. \*The number of pairwise associations in year 1 that could be re-established in year 2 was 152.

	Pupping site displacement of both mothers						
	> 0m	> 10m	> 20m	> 30m	> 40m	> 50m	> 60m
Count of pairwise associations present in both of year 1 and year 2	15	8	7	6	6	3	1
Probability of an association present in year 1 being re-established in year 2*	0.099	0.053	0.046	0.039	0.039	0.020	0.007

The results presented here differ from those presented in Pomeroy et al. (2005) as a revised data set was used here. Critically, in Pomeroy (2005) a total of 14 re-associations were observed out of a possible 126, whereas here 15 re-associations were observed out of a possible 152.

### 6.2.2 Null model

Given the observed data presented above it was necessary to calculate expected joint probabilities of mothers moving within given distance classes and remaining associated in order to test for active association. Grey seal mothers on North Rona are known to redistribute between breeding seasons due to three main processes other than sociality: site fidelity, temporal fidelity and site, or topography, preference (Pomeroy et al., 1999; Pomeroy et al., 1994; Twiss et al., 2000; Twiss et al., 2001). It is therefore possible to simulate mothers' redistributions. If social processes operate within the colony which allow mothers to coordinate their redistributions and so promote re-association (or alternatively avoidance) then the observed occurrence of re-association will differ from that simulated. In order to produce a simulation that contains realistic movements the following constraints were imposed:

#### Site fidelity.

The probability of an animal being redistributed to any other possible location was defined by the observed probability distribution of site fidelity distances. This probability distribution was constructed from 484 observed movements by 182 mothers pupping in consecutive years within the SA over the period 1985 to 2002 which had a median of 39m (Pomeroy, pers. com). The

simulation did not account for animals that either returned to the island but located outwith the SA or did not return to the island at all.

#### Site preference.

Grey seal mothers are known to locate preferentially in areas of certain topographic value. A proxy for the geographic distribution of suitable habitat was provided by the observed distribution of all animal locations in 2000. By constraining animals to use only actually used locations, topography choice within the simulation mirrors that observed.

#### Temporal fidelity.

The probability of temporal re-association due to observed changes in pupping dates between consecutive years was 0.754. This was therefore used as the probability for temporal re-association within the simulation (Pomeroy, 2005).

#### Simulation procedure

For each known mother in year 1 (1998 or 1999), the probability of moving to any observed location in 2000 was calculated from the site fidelity probability distribution in 10m bins. The probability of moving to each location was then divided by the number of locations within each 10m bin. The probability of moving to within any 10m bin therefore matched that of the site fidelity probability distribution. As each location within any 10m bin had an equal probability, site choice was represented by the spread of available locations within each 10m bin. Mothers from year 1 were then redistributed to an

available location due to the above calculated probabilities. This process was repeated 5000 times. It was then possible to calculate the probability that mothers who were associated in year 1 would re-associate in year 2 due to observed site fidelity and site preference. This was then multiplied by the probability of temporal re-association to provide a joint probability that mothers would move certain distances yet remain spatially and temporally associated. The above protocol was carried out using procedures custom written for this purpose by the author in R (R Development Core Team, 2004) (Appendix C). This procedure differs from that presented in Pomeroy et al. (2005) by including animals from both 1998 and 1999 in the simulation.

### 6.2.3 Results

The simulated probability that mothers who were associated in year 1 would move certain distances to a location in year 2 are shown in Table 6.2.3.1(A). The probability that mothers would re-associate spatially in year 2 given certain movements is shown in Table 6.2.3.1(B) and the probability that mothers would re-associate temporally in year 2 is shown in Table 6.2.3.1(C). The joint probability that two mothers, associated in year 1, would move certain distances and remain spatially and temporally associated in year 2 is shown in Table 6.2.3.1(D). The simulated data is summarised and presented alongside the observed data in cumulative distance classes in Table 6.2.3.1(E). Note that Table 6.2.3.1(E) also illustrates a slight difference between the joint probabilities of those mothers known in 1998 re-associating in 1999 and those mothers known in 1999 re-associating in 2000. From Table 6.2.3.1(E) it can be seen that the biggest difference in observed and expected probabilities occurs when females

**Table 6.2.3.1.** Simulated probability of re-association given certain movements, due to site fidelity, temporal fidelity and site preference for consecutive years between 1998 and 2000

**(A) Probability that two females will move a certain distance between pupping sites in consecutive years**

Distance moved (m)		Female A								
		0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80+
Female B	0-10	0.0128	0.0176	0.0160	0.0159	0.0128	0.0090	0.0075	0.0067	0.0138
	10-20	0.0181	0.0250	0.0229	0.0225	0.0178	0.0130	0.0109	0.0093	0.0196
	20-30	0.0162	0.0229	0.0210	0.0205	0.0165	0.0114	0.0101	0.0086	0.0179
	30-40	0.0162	0.0222	0.0208	0.0203	0.0157	0.0113	0.0095	0.0084	0.0174
	40-50	0.0127	0.0181	0.0164	0.0160	0.0127	0.0090	0.0077	0.0067	0.0139
	50-60	0.0090	0.0126	0.0117	0.0114	0.0091	0.0065	0.0054	0.0047	0.0100
	60-70	0.0077	0.0106	0.0099	0.0097	0.0077	0.0056	0.0046	0.0039	0.0082
	70-80	0.0066	0.0092	0.0084	0.0082	0.0066	0.0048	0.0039	0.0033	0.0071
80+	0.0138	0.0189	0.0179	0.0174	0.0139	0.0099	0.0083	0.0072	0.0151	

**(B) Probability that two females will move a certain distance between pupping sites in consecutive years yet remain spatially associated**

Distance moved (m)		Female A								
		0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80+
Female B	0-10	0.8492	0.6189	0.2770	0.0583	0.0028	0	0	0	0
	10-20	0.6246	0.4993	0.3026	0.1167	0.0272	0.0021	0	0	0
	20-30	0.2652	0.3018	0.3037	0.2035	0.0865	0.0233	0.0009	0	0
	30-40	0.0509	0.1189	0.2093	0.2217	0.1734	0.0783	0.0182	0.0008	0
	40-50	0.0028	0.0247	0.0910	0.1623	0.1828	0.1426	0.0648	0.0194	0.0001
	50-60	0	0.0020	0.0188	0.0759	0.1427	0.1628	0.1384	0.0703	0.0058
	60-70	0	0	0.0013	0.0191	0.0691	0.1336	0.1885	0.1596	0.0179
	70-80	0	0	0	0.0008	0.0132	0.0663	0.1645	0.1947	0.0522
80+	0	0	0	0	0.0002	0.0034	0.0217	0.0522	0.0843	

**(C) Probability that two females will move a certain distance between pupping sites in consecutive years yet remain temporally associated**

Distance moved (m)		Female A								
		0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80+
Female B	0-10	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754
	10-20	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754
	20-30	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754
	30-40	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754
	40-50	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754
	50-60	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754
	60-70	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754
	70-80	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754
80+	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754	0.754	

**(D) Joint probability that two females will move a certain distance between pupping sites in consecutive years yet remain spatially and temporally associated**

Distance moved (m)		Female A								
		0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80+
Female B	0-10	0.0082	0.0082	0.0033	0.0007	0.0000	0	0	0	0
	10-20	0.0085	0.0094	0.0052	0.0020	0.0004	0.0000	0	0	0
	20-30	0.0032	0.0052	0.0048	0.0031	0.0011	0.0002	0.0000	0	0
	30-40	0.0006	0.0020	0.0033	0.0034	0.0021	0.0007	0.0001	0.0000	0
	40-50	0.0000	0.0003	0.0011	0.0020	0.0017	0.0010	0.0004	0.0001	0.0000
	50-60	0	0.0000	0.0002	0.0007	0.0010	0.0008	0.0006	0.0002	0.0000
	60-70	0	0	0.0000	0.0001	0.0004	0.0006	0.0006	0.0005	0.0001
	70-80	0	0	0	0.0000	0.0001	0.0002	0.0005	0.0005	0.0003
80+	0	0	0	0	0.0000	0.0000	0.0001	0.0003	0.0010	

**(E) Joint probability summary in cumulative distance classes**

	Pupping site displacement of Female A and B						
	> 0m	> 10m	> 20m	> 30m	> 40m	> 50m	> 60m
1998-1999*	0.097	0.063	0.037	0.022	0.012	0.007	0.004
1999-2000*	0.086	0.054	0.031	0.018	0.010	0.006	0.004
1998-2000	0.091	0.058	0.034	0.020	0.011	0.006	0.004
Observed	0.099	0.053	0.046	0.039	0.039	0.020	0.007

\* These represent the output of the simulation for either the period 1998-1999 or 1999-2000 only

move and re-associate over a distance greater than 40m. However, this difference is not significant ( $G_{adj}=2.45$ ,  $df=1$ ,  $p>0.05$ ).

### 6.3 Re-sighting rates of resident mothers in 2002 and 2003

The remainder of this chapter is concerned with new data collected specifically for this thesis during the 2002 and 2003 breeding seasons. In these years all females within the pre-defined study areas (see Figure 2.1.1) were photographed and located throughout the breeding season (for survey schedule see Table 2.3.1.1). As the study areas were slightly different in 2002 and 2003, the results presented here refer to resident mothers from the study area as delineated in 2002 that were re-sighted in the study area as delineated in 2003. This difference in areas was taken into account in the simulation. Resident mothers were defined as those which were observed to give birth and raise a pup in the study area. Although not every animal encounter within the study area resulted in a positive identification, the identification rate throughout each season was high (83% of all animal encounters in 2002 and 93% of all animal encounters in 2003, see Table 2.3.1.1). As resident mothers were encountered multiple times during a season it is highly unlikely that any would be unidentified. It was therefore assumed that every resident mother that gave birth and raised a pup within the study area in 2002 and 2003 was known. As the study areas in 2002 and 2003 and the resident mothers therein constitute a sub-sample of the colony, however, it is necessary to examine the activity of these animals in the context of the colony as a whole.

#### 6.3.1 Observed and expected re-sighting rates

##### Quantification of expected re-sighting rates

The expected number of resident mothers observed in 2002 that would be observed as resident mothers again in 2003 was calculated by a simulation

incorporating site fidelity and preference. Here, the site fidelity probability distribution was constructed from all observed movements of animals present throughout the full extent of the SA in both 2002 and 2003. Site preference was modelled by restricting available locations to those in which mothers were actually observed to have a pup. This is in contrast to using all observed female locations as in Section 2 of this chapter. This is because some of those locations may be associated with females in transit to or from their chosen location and so provide an unrealistic representation of site choice. The best estimate of site choice is provided by the distribution of centroid locations (see Section 6.2.1.). However, centroid locations were not available for all mothers outwith the study area. As mothers do not move far from their original pupping site and pups are classified as being of stage 1 for two days from birth it was possible to approximate the distribution of centroid locations outwith the study area by sampling all locations of stage 1 pups at two day intervals (Redman, 2002), Chapter 3, Twiss, pers. comm.). Available locations were therefore restricted to those that were (i) observed centroid locations within the 2003 study area and (ii) observed locations of all stage 1 pups sampled at 2 day intervals outwith the 2003 study area.

#### Simulation procedure

For each resident mother in the study area in 2002, the probability of moving to any possible location both within and outwith the study area in 2003 was calculated following the procedure outlined in Section 6.2.2. Resident mothers from 2002 were then redistributed to available locations 5000 times. It was then possible to calculate the probability that mothers who were resident in

the study area in 2002 would return to the study area in 2003 due to observed site fidelity and site preference. The above protocol was carried out using procedures custom written for this purpose by the author in R (R Development Core Team, 2004) (Appendix D).

#### Colony-wide re-sighting rates

The above simulation only calculates the probability of return to the study area for animals that return to the island at all. Some animals may not return to the island in consecutive years (Pomeroy et al., 1994). Previous studies have found the re-sighting rate for well marked animals to be around 80%-90% (Pomeroy et al., 1994; Redman, 2002). Although the focus of this study was to identify individuals within the predefined study area considerable effort by the research group was also put into identifying animals outwith this area. The locations of all animals and identification of all known individuals within the Study Area and southern-most part of Fianuis South, as defined in Pomeroy et al. (1994), was undertaken daily during the 2002 and 2003 breeding seasons. In addition, the identification of known animals in Fianuis South and Fianuis North was undertaken on 6 dates in 2002 (one date of which was a dedicated identification survey, identification on the other dates being opportunistic) and 4 dates in 2003 (two of which were dedicated identification surveys). It was therefore possible to estimate the apparent return rate of animals to the island.

#### Results

There were 27 resident mothers in the study area in 2002 that were observed again as resident mothers in the study area in 2003. In total, 67 and 70

resident mothers were observed in the study area in 2002 and 2003 respectively. The observed return rate to the study area from 2002 to 2003 was therefore 40% (27 out of 67 mothers).

Of the 67 mothers observed in the study area in 2002, 51 (76%) were observed on the island, either with or without a pup, in 2003. The real breeding return rate may be lower if some of those animals observed did not give birth on the island or higher if some mothers were present but not observed, for instance if they were located in sites that were difficult to observe at the northern or southern extremities of the island.

The simulated mean and 95% confidence intervals of expected return rates to the study area due to observed site fidelity and preference can be seen in Table 6.3.1.1. This is multiplied by 100%, 90% and 76% to take into account various possible return rates to the island itself. The observed return rate of 40% is within the simulated 95% confidence interval for resident mothers observed in the study area in 2002 returning to the study area in 2003 when the probability of returning to the island is 76%.

Table 6.3.1.1 Simulated return rates to the study area in 2003 by resident mothers observed in the study area in 2002.

	Colony-wide resight rate		
	100%	90%	76%
Mean simulated return rate to study area (2002-2003)	59%	53%	45%
95% confidence interval of above	50%-68%	45%-61%	38%-51%

### 6.3.2 Movement between areas of the North Rona colony

Resident mothers that were observed in the study area in only one of the 2002 or 2003 breeding seasons may have been present on the island but resident outwith the study area in the other year. As much effort went into locating known mothers outwith the study area (see Section 6.3.1) it is possible to estimate the proportion of animals that used the study area in one year and a different part of the North Rona colony in another.

There were 40 out of 67 resident mothers in the study area in 2002 that did not return to the study area in 2003 (Table 6.3.2.1(A)). Of these, 24 females were observed on North Rona in 2003 but outwith the study area and 16 were not observed at all. Of those that were observed outwith the study area, 19 were observed with a pup. Although 16 animals were not re-sighted on the island in 2003, this does not mean they were not there. The maximum estimate for the percentage of resident study area mothers in 2002 that may have returned to raise a pup in another area of the island is therefore 60% (40 out of 67) and the minimum estimate is 28% (19 out of 67). 4% of all re-sighted mothers (2 out of 51) were observed to move to Fianuis North (FN) between 2002 and 2003. Interestingly, these two individuals were temporally and almost spatially associated in 2002 (spatial separation of centroid locations = 23m), and temporally and spatially associated in 2003, approximately 700m away from their locations in the previous year.

There were 43 out of 70 resident mothers in the study area in 2003 that were not resident mothers in the study area in 2002 (Table 6.3.2.1(B)). Of these, 18 females were observed on North Rona but outwith the study area in 2002. Of these, 10 were observed with a pup. The upper estimate for mothers moving into

the study area from other areas on the North Rona colony from 2002 to 2003 is therefore 61% (43 out of 70) and the lower estimate is 14% (10 out of 70). The chance that animals were present on the island in 2002 but not observed will be increased if mothers were not 'known' before 2003. There were 25 out of 70 resident mothers (36%) in 2003 that were not seen in 2002. 13 of these (19% of 70) were not 'known' before 2003. No animals were observed to move to the study area from FN.

Table 6.3.2.1 Locations in the other year of resident mothers observed in the study area in one of 2002 or 2003.

(A) Resident mothers in study area in 2002 (n=67) who were:

	number	%
<i>not</i> resident mothers in study area in 2003	40	60%
observed outwith study area in 2003	24	36%
observed with a pup outwith study area in 2003	19	28%
not observed in 2003	16	24%
proportion of re-sighted mothers observed with pup in FN in 2003	2 / 51	4%

(B) Resident mothers in study area in 2003 (n=70) who were:

	number	%
<i>not</i> resident mothers in study area in 2002	43	61%
observed outwith study area in 2002	18	26%
observed with a pup outwith study area in 2002	10	14%
not observed in 2002	25	36%
not 'known' from before 2003	13	19%

The extent of mixing between FN and the study area has not previously been known. Although the true extent is still not known the data here provide an indication as to what it might be. If those animals that were resident within the study area in 2002 but not observed in 2003, did in fact return to the colony it is most likely that they located in FN, where the identification effort was least. In turn it is likely that at least some animals 'known' for the first time in 2003 may have been located but not observed in previous years in FN. 4% of re-sighted

animals were known to move from the study area to FN, but the above suggests that the real mixing figure may be slightly higher. Of course, some of the animals that were not observed in either year may have been located outwith FN but not observed or may have not been on the island at all. Nevertheless it is possible that between 4% and somewhere around 19-24% of animals change pupping location between FN and the study area between years.

#### 6.4 Social Stability

The description of pair-wise associations and their maintenance as in Section 2 of this chapter is instructive for elucidating cohesion between two specific individuals. However, individuals often have more than one associate. Therefore, while an individual may appear to be socially cohesive in maintaining or re-establishing one particular association, it may also be involved in the discontinuation or start up of many others. Any effect of sociality may therefore encompass the entire set of associations that an individual is involved in. As such, describing a sub-set of the pair-wise associations that an animal may maintain is inadequate to describing its sociality. Here, a fully inclusive summary of sociality is provided by calculating the social stability of each individual and its neighbours between consecutive breeding attempts.

Individual based social stability was calculated using the Jaccard index (I-SSj) as described in Chapter 4. The spatial scale of association within an entire breeding season was estimated to be 20m as described in Chapter 3. Social stability was therefore only measurable for individuals for which all neighbours within 20m were known in 2002 and 2003.

##### 6.4.1 Quantification of between-year social stability for individuals

There were 67 resident mothers within the study area in 2002 and 70 in 2003. Although 27 of those resident mothers were present in both 2002 and 2003, not all neighbours could be known for those which resided near the edge of the study area. Therefore only the 18 animals who were present in both years and for which all neighbours within 20m were known were considered further in this analysis. There was a variance of I-SSj values between the 18 resident

mothers (Figure 6.4.1.1). The mean I-SSj value was 0.09 with a range of 0.19 (0.0 to 0.19). The geographic locations of I-SSj values from 2002 to 2003 are shown in Figure 6.4.1.2.

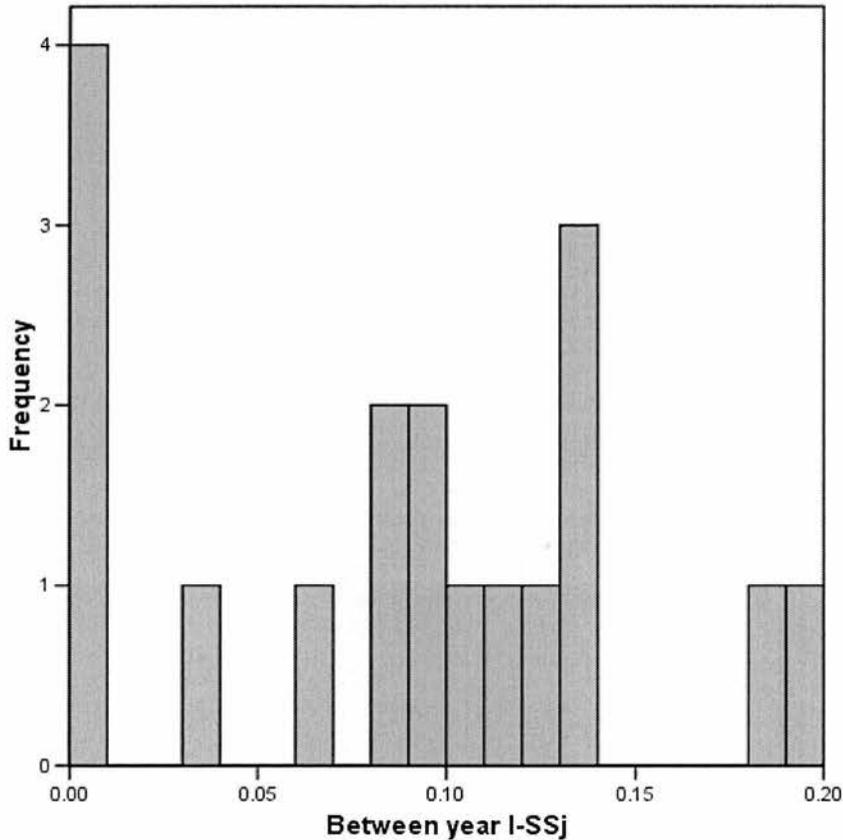
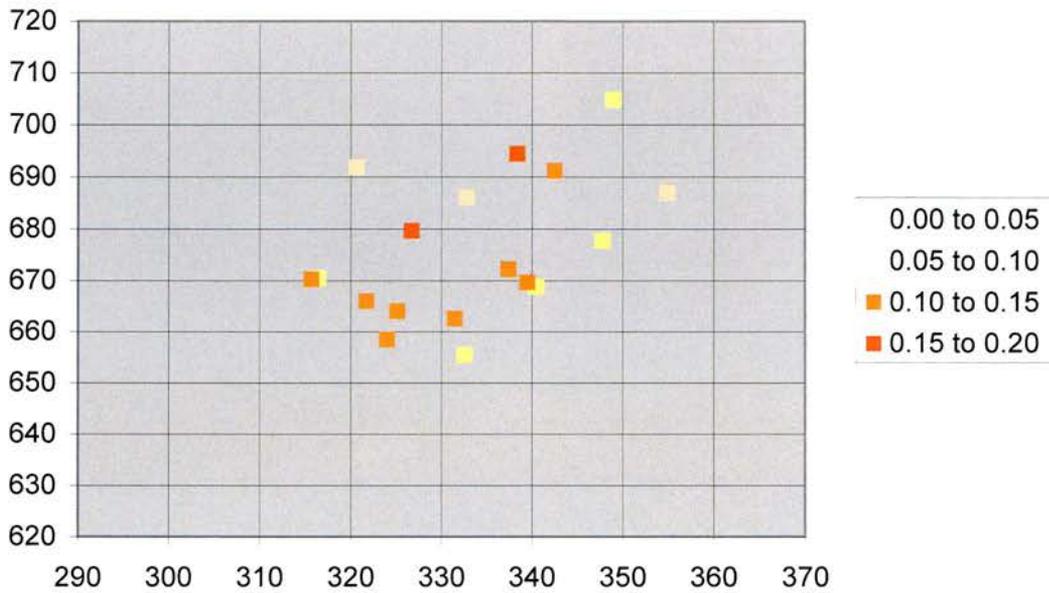


Figure 6.4.1.1 Frequency distribution of between year I-SSj values for 18 resident mothers present in the study area in 2002 and 2003

#### 6.4.2 Null model

In order to test whether observed I-SSj values differed from that expected under random re-colonisation of the colony it was necessary to calculate expected I-SSj values through simulation. As in previous sections of this thesis realism was achieved within the simulation by constraining behaviour to emulate

**(A) Locations in 2002 of mothers and their between year I-SSj values for 2002 to 2003**



**(B) Locations in 2003 of mothers and their between year I-SSj values for 2002 to 2003**

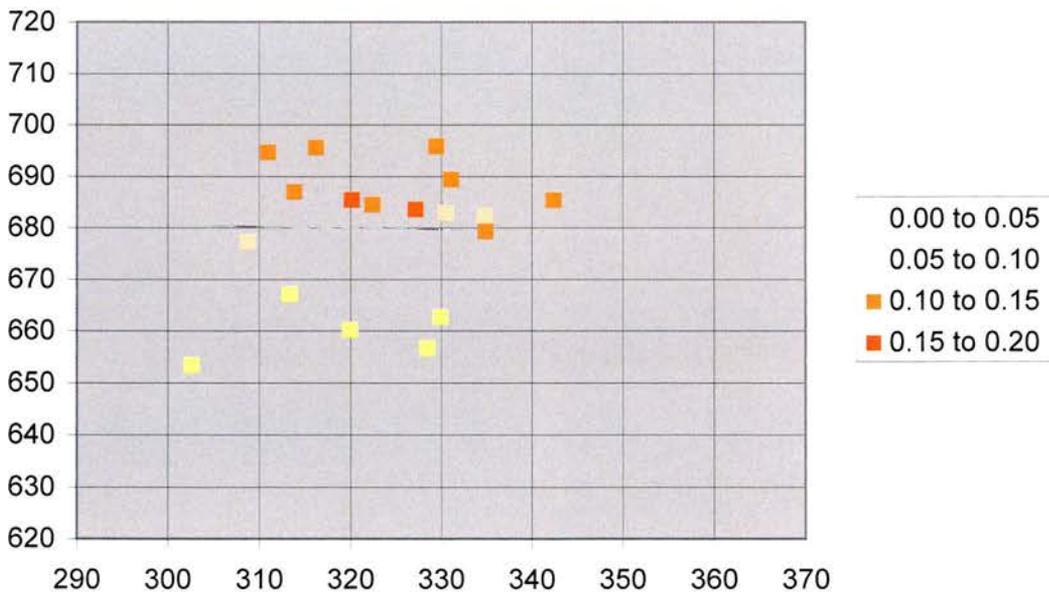


Figure 6.4.1.2. Geographical locations in 2002 and 2003 of resident mothers and their between year I-SSj values from 2002 to 2003. Axes represents OSGB eastings (prefix 181\*\*\*) and northings (prefix 1032\*\*\*). Map units are in metres.

observed site fidelity, temporal fidelity and site preference. However, several improvements were made over the simulation described in Section 6.2.

1. As in Section 6.3 of this chapter, site preference was restricted to locations in which mothers were observed with a pup, rather than all locations in which females were observed. This reduces any geographical bias to areas commonly used by females in transit.

2. The I-SSj for each resident mother was tested against a unique distribution of I-SSj values from a simulation based on her observed site and temporal fidelity. This is in contrast to testing individuals against a global distribution simulated using all mothers as in Section 6.2. This is an important step as the social stability that an individual is likely to experience may depend on factors unique to that individual. Specifically, if an individual locates in an area where the distribution of possible locations is limited, then I-SSj would more likely be higher than if that individual located in the centre of a uniform distribution of possible locations. This is because if locations are restricted (for instance at the edge of the colony) then chance coordination of movement will be higher. Equally, sociality may also depend on the extent of change of individuals' pupping dates.

3. The output of the simulation here decouples the probability of movement from the probability of sociality. The output in Section 6.2 of this chapter describes the probability that two animals should both move certain distances *and* re-associate. However, as the probability of movement is already known from the observed site fidelity distribution, it is more instructive to ask about the likelihood of re-association, and in turn I-SSj, given certain movements.

4. Temporal fidelity was modelled implicitly within the simulation, rather than being an external multiplier (i.e. 0.754 in Section 6.2). Therefore, the between year change in each animals' pupping date was modelled by drawing values from the observed probability distribution of temporal fidelity.

5. New identities were created within the simulation so that new associations could be formed and therefore I-SSj including re-association, dis-association and new association be calculated.

The output from this simulation therefore describes the I-SSj value that an individual may expect given its observed location, movement and change in pupping date. The following constraints to behaviour were imposed:

#### Site preference

Site preference was modelled as in Section 6.3.1 of this chapter by restricting access only to locations that were (i) observed centroid locations within the 2003 study area and (ii) observed locations of all stage 1 pups sampled at 2 day intervals outwith the 2003 study area.

#### Site fidelity

The site fidelity probability distribution was constructed from all movements of mothers that were observed both within and outwith the study area in 2002 and 2003.

### Temporal fidelity

The temporal fidelity distribution was constructed from all changes in pupping date by all mothers observed both within and outwith the study area in 2002 and 2003.

### Pupping date distribution

New identities created within the simulation were assigned a pupping date from the observed distribution of all pupping dates in 2003.

### Simulation procedure

The following simulation was carried out separately for each of the 18 focal mothers observed in both 2002 and 2003 for whom all associates within 20m and 9 days were known. The location and pupping date of the focal mother in the simulation output was the same as her observed location and pupping date in 2003. For each other resident mother within the study area in 2002, the probability of moving to any possible location both within and outwith the study area in 2003 was calculated from the site fidelity probability distribution and available locations as described in Section 6.2.2. Resident mothers from 2002 were then redistributed to a location due to the above calculated probabilities. The pup date of each mother was then altered due to the observed temporal fidelity probability distribution. New identities were created within the remaining list of possible locations that had not been colonised. Pupping dates for these new identities were drawn from the observed distribution of pupping dates. It was then possible to calculate the I-SSj value for the focal mother between 2002 and the simulated data set. This was repeated 5000 times for each

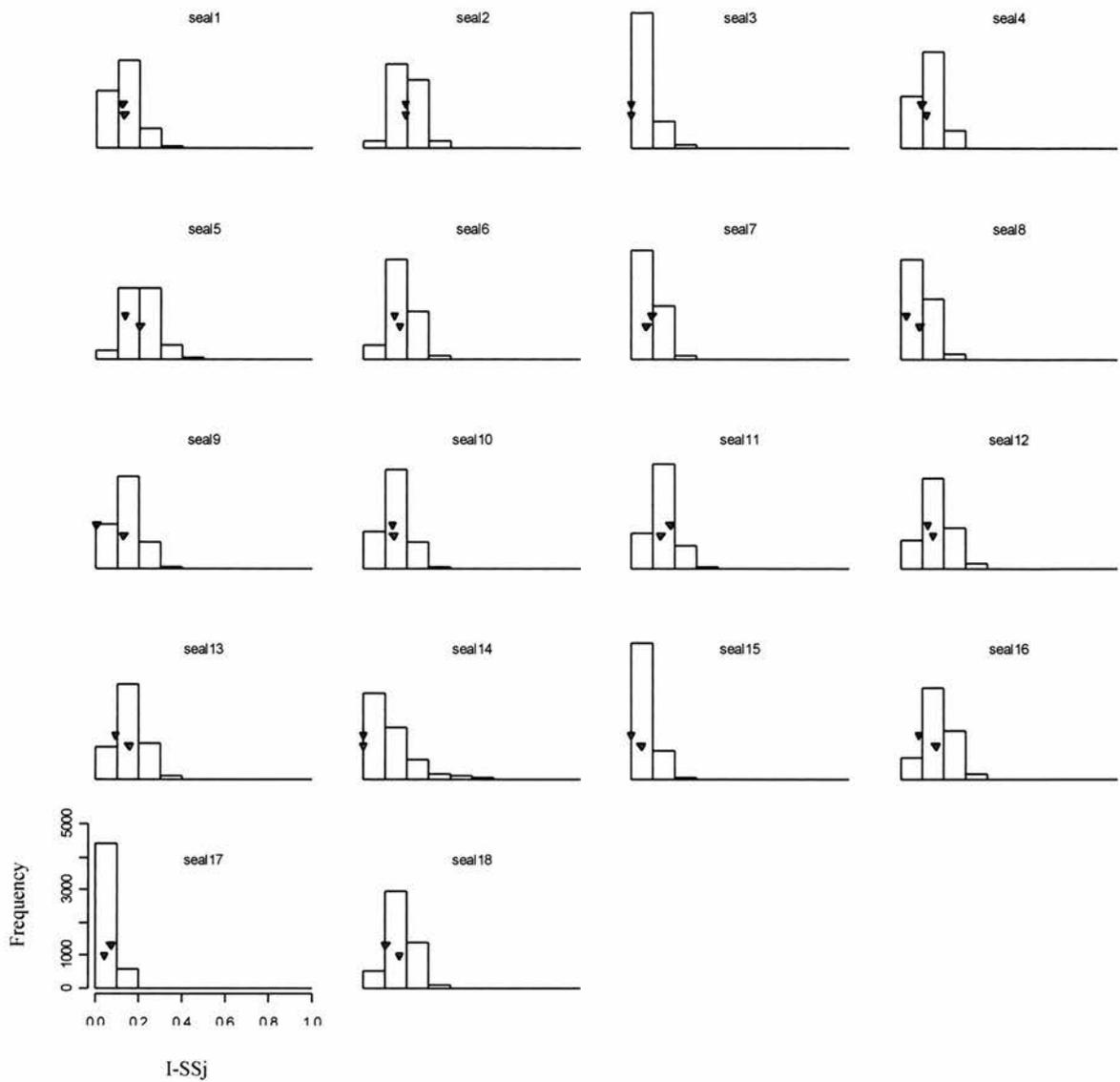
focal mother to provide a distribution of expected I-SSj values. The above protocol was carried out using procedures custom written for this purpose by the author in R (R Development Core Team, 2004) (Appendix E).

### Simulation results

The distribution of simulated I-SSj values for each individual can be seen in Figure 6.4.2.1. The magnitude of observed I-SSj between 2002 and 2003 is marked by a green triangle and the median of the simulated distribution is marked by a red triangle. Overall, there appears to be little difference between observed and expected I-SSj values. One of the eighteen individuals tested (seal9) had an observed value that was significantly lower than the simulated distribution at  $\alpha = 0.05$ . However, this difference was not robust to Bonferroni correction ( $\alpha=0.0028$ ).

### 6.4.3 Predictors of social stability and the influence of social stability on maternal performance

Although the observed values of I-SSj measured between 2002 and 2003 do not appear to differ from that expected by chance, variance in I-SSj may still be affected by or have an effect upon other measurable variables. Here, between year I-SSj values are investigated in relation to topographic variables, changes in pupping site and date, within year I-SSj and maternal performance. For details of the calculation of these variables see Chapter 5.



**Figure 6.4.2.1.** Distributions of simulated median between year I-SSj values for 18 resident mothers present in the study area in 2002 and 2003. Histograms display the median simulated values from 5000 simulations for each individual. The observed I-SSj value for each individual is plotted as a green triangle and the median simulated value as a red triangle.

Topographic variables

I-SSj was investigated for correlation with values of cost distance to pools, cost distance to the sea, elevation and slope for the area in which each individual was located in 2003. In accordance with the geographic location of individuals and their I-SSj values in Figure 6.4.1.2, higher I-SSj values appear only to be associated with lower cost distance to the sea (Coeff.=-0.007,  $t(16)=-2.32$ ,  $p<0.05$ ) and lower values of slope (Coeff.=-0.01,  $t(16)=-3.97$ ,  $p<0.05$ ) (Table 6.4.3.1(A)). That is, individuals with higher I-SSj values were located nearer to the North and East of the study area where access to the sea is greater and the terrain is flatter.

Behavioural variables

I-SSj was also investigated for correlation with values for each mother of: pupping synchrony and aggression for her location in 2003, her number of associates in 2003, her mean pupping date, site and temporal fidelity between 2002 and 2003, and her within year I-SSj values in 2002 and 2003. I-SSj appears to be higher when the number of associates is also high (Coeff.= 0.005,  $t(16)=5.88$ ,  $p<0.05$ ) and the pupping date is earlier in the season (Coeff.= -0.005,  $t(16)=-2.59$ ,  $p<0.05$ ) (Table 6.4.3.1(A)).

Multivariate models explaining social stability

A maximal model including all explanatory variables on I-SSj and a minimal model selected by minimisation of the AIC were created. Although both models were significant (Max:  $\text{adj}R^2:0.941$ ,  $F(12,5)=23.52$ ,  $p<0.05$ ) (Min:  $\text{adj}R^2:0.955$ ,  $f(10,7)=36.94$ ,  $p<0.05$ ) they provided no obvious mechanism for the

Table 6.4.3.1. Factors influencing between year I-SSj and maternal efficiency

(A) Individual relationship between variables and between year I-SSj:

Variables:		Model:						
Model		Coeff.	Std.Error	t	p	Adj.R <sup>2</sup>	F(1,16)	p
1	Intercept	0.091	0.048	1.917	0.0733			
	Cost distance to pool	-0.002	0.042	-0.054	0.9578	-0.062	0.003	0.9578
2	Intercept	0.231	0.063	3.690	< 0.05			
	Cost distance to sea	-0.007	0.003	-2.322	< 0.05	0.205	5.391	< 0.05
3	Intercept	0.210	0.084	2.511	< 0.05			
	Elevation	-0.009	0.006	-1.473	0.1602	0.064	2.170	0.1602
4	Intercept	0.236	0.038	6.125	< 0.05			
	Slope	-0.010	0.003	-3.974	< 0.05	0.465	15.790	< 0.05
5	Intercept	0.006	0.058	0.098	0.923			
	Synchrony	0.422	0.284	1.484	0.157	0.066	2.203	0.1572
6	Intercept	0.031	0.056	0.551	0.589			
	Aggression	0.169	0.158	1.071	0.300	0.009	1.148	0.2999
7	Intercept	-0.071	0.028	-2.499	< 0.05			
	Number of associates	0.005	0.001	5.875	< 0.05	0.664	34.520	< 0.05
8	Intercept	0.263	0.068	3.844	< 0.05			
	Mean pupping date	-0.005	0.002	-2.594	< 0.05	0.252	6.727	< 0.05
9	Intercept	0.081	0.021	3.920	< 0.05			
	Temporal fidelity	-0.002	0.005	-0.506	0.61978	-0.046	0.256	0.6198
10	Intercept	0.133	0.031	4.302	< 0.05			
	Site fidelity	-0.002	0.001	-1.606	0.128	0.085	2.578	0.1279
9	Intercept	0.143	0.037	3.899	< 0.05			
	Within year I-SSj 2002	-0.144	0.090	-1.608	0.12746	0.085	2.585	0.1275
10	Intercept	0.143	0.042	3.442	< 0.05			
	Within year I-SSj 2003	-0.159	0.114	-1.395	0.18214	0.053	1.945	0.1821

(B) Maximal model explaining I-SSj:

AIC: -148.54

Variable		Model:						
		Coeff.	Std.Error	t	p	Adj.R <sup>2</sup>	F(12,5)	p
	Intercept	-0.255	0.076	-3.354	< 0.05			
	Cost distance to pool	0.043	0.019	2.303	0.070			
	Cost distance to sea	-0.015	0.005	-3.147	< 0.05			
	Elevation	0.016	0.008	1.968	0.106			
	Slope	0.009	0.004	2.295	0.070			
	Number of associates	0.008	0.001	7.514	< 0.05			
	Synchrony	0.102	0.206	0.494	0.642			
	Aggression	-0.086	0.111	-0.769	0.477			
	Mean pupping date	0.001	0.001	1.092	0.325			
	Site fidelity	0.000	0.001	-0.217	0.837			
	Temporal fidelity	-0.002	0.002	-0.646	0.546			
	Within year I-SSj 2002	0.184	0.047	3.921	< 0.05			
	Within year I-SSj 2003	-0.286	0.094	-3.054	< 0.05	0.941	23.52	< 0.05

(C) Minimal model explaining I-SSj based on minimisation of the AIC:

AIC: -151.35

Variable		Model:						
		Coeff.	Std.Error	t	p	Adj.R <sup>2</sup>	F(10,7)	p
	Intercept	-0.243	0.061	-3.958	< 0.05			
	Cost distance to pool	0.041	0.013	3.166	< 0.05			
	Cost distance to sea	-0.017	0.004	-4.752	< 0.05			
	Elevation	0.016	0.007	2.342	0.052			
	Slope	0.011	0.003	4.403	< 0.05			
	Number of associates	0.008	0.001	10.063	< 0.05			
	Aggression	-0.053	0.057	-0.933	0.382			
	Mean pupping date	0.001	0.001	1.425	0.197			
	Temporal fidelity	-0.002	0.001	-1.572	0.160			
	Within year I-SSj 2002	0.195	0.037	5.351	< 0.05			
	Within year I-SSj 2003	-0.322	0.056	-5.797	< 0.05	0.955	36.94	< 0.05

(D) Relationship between I-SSj and maternal efficiency:

Variables:		Model:						
Model		Coeff.	Std.Error	t	p	Adj.R <sup>2</sup>	F(1,2)	p
	Intercept	0.600	0.094	6.413	< 0.05			
	I-SSj	0.099	0.708	0.141	0.9011	-0.485	0.020	0.9011

promotion of I-SSj within the colony (Table 6.4.3.1(B-C)). The minimal model was only able to discount 2 variables, and the degrees of freedom for both models indicate over-fitting. In addition there appears to be a conflict of influence between the within year I-SSj in 2002 and 2003 explanatory variables. Higher within year I-SSj in 2002 is associated with higher between year I-SSj (Coeff.=0.195,  $t(7)=5.35$ ,  $p<0.05$ ), yet higher within year I-SSj in 2003 is associated with lower between year I-SSj (Coeff.=-0.322,  $t(7)=-5.80$ ,  $p<0.05$ ). This can also be seen in a comparison of the location of individuals with high between year I-SSj (Figure 6.4.1.2) and the areas of depressed within year A-SSj shown in Figure 5.4.2.3-4.

#### Effect of social stability on maternal performance

There was no observable effect of between year I-SSj on maternal efficiency (Coeff.=0.099,  $t(2)=0.14$ ,  $p=0.90$ ) (Table 6.4.3.1(D)). It should be noted that the sample size here was very low, being only four data points, and so this test is far from conclusive.

## 6.5 Discussion

The assessment of long term pair-wise associations presented in Pomeroy et al. (2005) provided new insight into the possibilities of grey seal social organisation. A simulation describing the expected probability of two mothers both moving certain distances between pupping attempts and remaining associated could not explain observed patterns of movement and association when movement was over 40m. Therefore, animals were observed to move further than the median site fidelity distance and associated more often than would be expected by chance. This suggested that some mothers were actively choosing to re-associate with others with whom they had been associated before. However, social fidelity was indiscernible from site fidelity when movements were less than 40m.

This finding was not replicated in the analysis presented here. There were two fundamental differences between these two studies. The data set was revised for use in this study thus providing a new set of known mothers and consequently a new set of associations. In addition, where Pomeroy et al. (2005) calculated expected probabilities of movement and association by simulating the behaviour of known mothers from 1999 only, in this study the behaviour of known mothers from 1998 and 1999 were simulated.

A limitation of the study of pair-wise associations was that only a restricted part of the social environment experienced by each known mother was targeted. In turn, as only a subset of animals within the area under study were known, only a limited view of the social structure across the colony was gained. If the act of re-association is important to an individual then it is likely that the loss and gain of associations may also be important. Further detail was therefore

sought by examining I-SSj, a composite measure of all the associations that animals are involved in. However, the effort involved in such an investigation necessarily limits its scope.

A restricted area was defined in which all individuals could be identified, and so all associations be assessed. The rate at which individuals return to breed in this area is defined by site fidelity and the return rate to the breeding colony itself. The rate of return to the island found here was lower than that reported previously (Pomeroy et al., 1994; Redman, 2002). A outbreak of the phocine distemper virus (PDV) affected populations in the North Atlantic in 2002. Although this virus can be fatal to harbour seals it is known to have little effect on grey seals at either the individual or population level (Carter et al., 1992; Jensen et al., 2002; Pomeroy et al., 2005a). It is unlikely that PDV would have effected return rates of grey seals to North Rona and the reason for reduced re-sighting rates in this study is unexplained. If this lower re-sighting rate is indicative of lower return rates to the island then this may have resulted in a depression of I-SSj.

The rate of return by mothers to the study area did not differ from that expected, given the rate of return to the island, suggesting animals were neither avoiding nor returning preferentially to the area. Observed movements between the study area and the rest of the colony showed that mixing occurred. The extent of mixing, specifically between Fianuis North and the study area has previously been unknown. Although the real extent of mixing is still unknown the data presented here provide the first indication that somewhere between 4% and 24% of animals may change pupping site between these two areas between years. In addition, the use of genetic analysis may be useful in assessing whether

any of these individuals are from other breeding sites and so provide further insight into the extent of migration between colonies (Allen et al., 1995).

A variance in the I-SSj experienced between consecutive breeding attempts was found for mothers who returned to the study area. Crucially, however, there was little evidence that this variation deviated from chance. Only one animal did provide possible evidence of active social behaviour and this was in avoidance of previous associates.

While little evidence was found for active social organisation this is in accord with findings from the assessment of pair-wise association. While some evidence has been presented for active re-association occurring when site fidelity distances are large (although not corroborated in this study), social stability was only quantified within a restricted geographical area and so limited to individuals who's site fidelity distances were small. Therefore, what was gained in detail by measuring social stability was lost in the observed breadth of site fidelity behaviour. The social stability results presented here therefore agree both with the lack of active pair-wise re-associations presented here and the lack of active pair-wise re-associations presented previously when site fidelity movements were small (Pomeroy et al. 2005).

In the transition to measure I-SSj, improvements were also made to the methodology of testing sociality. The simulation output for the probability of pair-wise re-association differed slightly between the periods 1998-1999 and 1999-2000. This is because the animals involved in associations in 1998 were distributed differently to those in 1999. In using a global estimate of the probability of re-association from 1998-2000, then, animals were not being tested in a way specific to their individual circumstance. This illustrates the need for

individual testing of sociality in a way that is tailored to the possibilities available to each individual.

Whether actively or passively promoted, variance in I-SSj may be related to other parameters influential to grey seal breeding behaviour. I-SSj appeared higher in an area with moderate access to the sea and low slope, but not necessarily good access to pools, the topographical resource thought to be most influential to seal distribution (Twiss et al., 2002; Twiss et al., 2000). Therefore between year I-SSj does not appear to be enhanced in areas of good topographic quality. This would be likely if individuals are attracted to return to good areas, as suggested by site fidelity due to site preference. It is possible that competition for access to such habitat serves to regulate the potential for I-SSj. Alternatively, although access to pools varied across the study area perhaps availability of this resource was adequate in all areas that seals occupied, and so no effect on I-SSj was observed. I-SSj was also higher earlier in the season and when the number of associates was high. It is likely that the more associates an individual has, the more likely it is that one of those has been an associate before. However, in having more associates, it is likely that any benefit of re-association be diluted by the presence of others.

If sociality, a process built on short term interactions (Hinde, 1976), is operating it would seem likely to do so over various time scales. Short term I-SSj was described within breeding seasons in Chapter 5. If relationships are built up over time it would seem possible that animals experiencing high I-SSj within a season may attempt to experience high I-SSj between seasons. There was no conclusive evidence that increased within year I-SSj lead to increased between year I-SSj or vice versa.

Grey seal mothers have been observed to pup with previous associates on many occasions. During this study two individuals were observed to pup near each other in two years after site fidelity displacements of hundreds of meters. Such anecdotal evidence can be very compelling but further investigation suggests that active long term sociality may be more limited in its extent. If social bonding was active between consecutive breeding seasons then it would likely also extend over longer periods of time, allowing any benefits of such to accrue. However, in the study of pair-wise associations, none were present over all of the three years under study (Pomeroy et al., 2005). It seems that the most compelling evidence for the formation of long term associations would be provided by repeat associations and high social stability over a series of breeding attempts. Indeed, social stability may not be evident on the temporal scale over which this study was conducted. Grey seals are long lived animals with a reproductive life-span in excess of 20 years (Hewer, 1964). It is possible that patterns of association may only be apparent when considered over an animal's reproductive life.

The apparent lack of influence of sociality on grey seal site selection does not disprove its presence, as there are other pressures affecting seal breeding behaviour. Site fidelity and social fidelity are necessarily difficult to separate if the same sites are associated with the same individuals. As the tests of sociality presented here were based on observed site fidelity, which may have a social component, then the tests used may be over conservative. However, if social stability was an important influence on site fidelity then it may be expected that the scale on which site fidelity operates would be similar to the spatial scale of association. Site fidelity, though, generally operates over a larger scale

(Pomeroy et al., 1994; Pomeroy et al., 2005b). The site choice made by a grey seal mother will necessarily depend on the availability of locations at the time which she arrives. Site fidelity then, and indeed the possibility for social fidelity may depend also on the timing of arrival. As grey seals are capital breeders it would seem overly costly to reside permanently within a single location for any considerable period before being ready to pup. If the precise timing of breeding is outwith an animals control then stochasticity may enter into the process of site selection and so the possibility for site and social fidelity. The physiological constraints to temporal fidelity may therefore be a limiting factor to the promotion of sociality between grey seal mothers between years. Although mothers infrequently take up permanent residence at their pupping location more than a day or so before pupping, they are often seen on the colony up to 20 days previously (Pomeroy et al., 1999; Pomeroy, pers. comm., pers. obs.). It is possible that pre-emptive site selection or prospecting of potential associates is taking place during this period. The interplay between site fidelity and social fidelity may therefore be a complex one. Breeding site selection by a grey seal mother may depend both on the availability of preferred habitat and the availability of associates. A preference for topographical resource over social association and limited temporal control of breeding may act to limit the potential for re-associations and social stability.

# **Chapter 7**

## **General discussion**

7.1 How social are female grey seals?

This study has investigated female grey seal social organisation within the North Rona colony on a variety of levels. The distance over which animals were likely to influence and be influenced by the behaviour of others was estimated to be 10m during a season and 20m over a whole season (Chapter 3). This distance describes the separation distance over which animals were considered to be associated. Female grey seals experience a turnover of associates both within a breeding season and between breeding seasons. A measure of social stability (SS<sub>j</sub>) was selected with which to describe the change of associations through time (Chapter 4).

When measured within years, areas of both consistently high and consistently low levels of social stability were identified (Chapter 5.2). Some of these areas appeared more extreme in social stability values than could be explained by a model including observed patterns of site choice, inter-survey movements and temporal residence (Chapter 5.4). Areas of increased social stability were also those well populated by animals at different stages of lactation, towards the centre of the colony and with moderate access to pools (Chapter 5.5). Measures of individual specific within year social stability also illustrated both animals that experienced consistently high levels of social stability and animals that experienced consistently low levels of social stability (Chapter 5.2). Again, some measures of individual social stability appeared more extreme than would be expected from the null model (Chapter 5.4). These findings suggest that individuals may be able to influence the social environment that they experience depending on where they reside and who they associate with. Although this social organisation may be influenced by non-social

processes, at least some appears to be a direct result of active social behaviour. In addition, a trend was found for increased maternal performance with increased social stability (Chapter 5.6)

The probability that grey seal mothers associated in one year would move certain distances and re-associate in the next was quantified (Pomeroy et al. (2005), Appendix B). Comparison of observed probabilities with those generated from a null model incorporating site fidelity, site choice and temporal fidelity suggested that pairs of associated mothers were more likely to move to a pupping site over 40m away from their previous pupping site and re-associate in consecutive years than would be expected by chance. However, this result was not replicated when a more extensive data set and modelling process were used (Chapter 6.2). Measures of between year social stability for mothers which were present over consecutive years provided little evidence of deviation in social stability values from a null model incorporating site fidelity, site preference and temporal fidelity (Chapter 6.4). However, this study may have been limited by the geographical extent over which measures could be made. In order to calculate between year social stability for an individual, all associates within consecutive years must be known. In identifying all identities within an area the first, although very approximate, estimate of possible mixing between the two main breeding areas on North Rona was estimated to be somewhere between 4% and 24% (Chapter 6.3).

This body of evidence suggests that grey seal females do display active social behaviour at least to some extent within the breeding colony. This social organisation appears to allow some individuals to experience a more stable social environment through maintaining association with others. Such social behaviour

is clearly more complex than simple aggregation of animals on the colony, but nevertheless appears only to operate at a low level, and perhaps only between a few individuals.

## 7.2 Is sociality a selective advantage to female grey seals?

In a study of the reproductive success of grey seal mothers on North Rona, 75% of the variation in pup mass at weaning was unexplained by maternal mass, maternal length, duration of lactation or year (Pomeroy et al., 1999). A further study on the Isle of May suggested that behavioural investment in offspring, which may account for some of the unexplained variance in reproductive performance, was related to the topographic quality of pupping sites (Twiss et al., 2000). In this thesis, it was hypothesised that variance in social behaviour may explain some of the variance in reproductive success, through possible advantages of aggression reduction between familiar individuals (Utne-Palm & Hart, 2000). The primary limitation to reproductive success is the energy store that females bring with them to the colony with which to subsist and feed their pup (Pomeroy et al., 1999; Trillmich, 1996). Cooperative behaviour in the form of aggression reduction may therefore provide a more 'harmonious' social environment which in turn may allow a more efficient transfer of that energy to the pup. This is in addition to fewer risks of injury to or separation of mother and pup which may also affect reproductive success (Anderson et al., 1979; Baker et al., 1998). However, in this study no evidence was found for a relationship between aggression and social stability. Despite this there was some evidence, albeit inconclusive, that increased social stability may be associated

with increased maternal efficiency, a proxy for reproductive success (Chapter 5.6).

Reproductive success has been shown to vary within a social context in other species. Dominance is most often associated with increased reproductive success (Reiter et al., 1981; Ellis, 1995; Alados & Escos, 1992), although this is not always the case (Verhulst & Salomons, 2004). Dominance hierarchies, however, operate on a more complex level than grey seal sociality appears to, and aggression reduction is the most obvious direct advantage that grey seals may benefit from. However, observed levels of aggression were very low within the colony and so the sample size with which to test this hypothesis was limited.

It is also possible that observed behavioural aggression is not the best indicator of social advantage. That is, effects of social stress may operate at the more difficult to observe psycho-social and physiological levels. Socially induced stress is known to adversely affect human health and reproduction, being associated with spontaneous pre-term birth, birth of small infants and inferior parenting (Wadhwa et al., 2001; Feeley et al., 2005; Dejin-Karlsson et al., 2000; House et al., 1988). The effects of socially induced stress also have long-term adverse affects in animal reproduction. Experimental manipulation of social stability was said to be a weak stressor in relation to more obvious forms of physical stress (eg, heat or restraint) in guinea pigs (Kaiser & Sachser, 2001), although the supporting data is unpublished. Nevertheless it was found that maternal social stress was associated with masculinisation of female and delayed development of male offspring (Sachser & Kaiser, 1995; Kaiser & Sachser, 2001). In addition, baboon infant survival has been shown to be decreased when

social inclusion of mothers was low, even when rank and environmental conditions were taken into account (Silk et al., 2003).

Such evidence suggests that although sociality may appear to play a minor role in the reproductive process, it can have lasting consequences for lifetime reproductive success. It is possible that for grey seal mothers a small benefit to reproductive success in any one breeding attempt, such as a small increase in the probability of pup survival, may have a considerable benefit when accumulated over an animal's reproductive life-span. In addition, if the costs of reproduction are mediated through sociality in one year then this may act to increase the probability of success in the next year (Pomeroy et al., 1999). As such, sociality may become available as an adaptive mechanism for increased reproductive success.

Of course, advantages of sociality need not necessarily act through reproductive success directly. The breeding colony provides a definite opportunity for social behaviour to establish yet this may provide benefits to other aspects of grey seal life history. For instance, information exchange perhaps of feeding grounds, predator presence, or even the suitability of breeding colonies may all be possible advantages of social behaviour in this species and have consequences for lifetime reproductive success.

### 7.3 Social variability

Sociality varies both within and between taxa and in both life history and ecological contexts. Of the marine mammals, cetacean societies have received by far the most attention, (for example: (Bejder et al., 1998; Coakes & Whitehead, 2004; Lusseau & Newman, 2004)). Cetaceans are often

characterised by fission-fusion societies, whereby either individuals or small groups of individuals temporarily aggregate with others to form larger groups (Coakes & Whitehead, 2004; Connor et al., 2000). This fission-fusion structure and the strength of short and long term social bonds have been described in many species using measures of individual pair-wise association (Whitehead & Dufault, 1999). Such work has not only provided insight into how social organisation varies across different species but also how sociality varies within species and even within populations. For instance, a review by Connor et al. (2000) suggests that some female dolphins in Shark Bay, Australia, and Sarasota, Florida, appear to be social while others appear to be solitary. In addition, the strength of male social bonds appears to vary both between these populations and with a population in the Moray Firth, Scotland. The reasons for such differences are not fully understood but may, for instance, be linked to the environment, to predation risks or to the use of resources.

Sociality has not been investigated to the same extent within pinnipeds and what attention there has been is typically focussed on inter-sexual relations or mother-pup bonds (Amos et al., 1995; McCulloch & Boness, 2000; McCulloch et al., 1999; Mathevon et al., 2004; Dobson & Jouventin, 2003). Otariid mother-pup bonds can be present over extended periods of time (Trillmich, 1981), requiring skills that may predispose individuals to other social relations, either whilst breeding or during other parts of the animals' life history (Insley et al., 2003). In the otariids, environmental pressures appear to produce a variety of rearing strategies (Trillmich, 1990). Most notably, subpolar species must wean their pups within 4 months due to the commencement of winter and migration of the prey on which they feed. Temperate and tropical species,

however, show much more flexibility in their rearing strategies which can extend into years. Ecology therefore has profound effects on social behaviour.

Grey seals breed at many sites across the Eastern and Western Atlantic and the Baltic seas (Boskovic et al., 1996). The environment in which they breed varies across this range from featureless sand banks (Boness & James, 1979), ice (Haller et al., 1996), rocky or sandy beaches, geos or caves and inland grassy arenas (Hewer, 1960), yet little is known of the variations in sociality between breeding populations and sites. On many breeding colonies, females commute to the sea during lactation in a way that they do not do on North Rona (Anderson & Harwood, 1985; Twiss et al., 2000). Such behaviour tends to lead to increased aggression (Anderson & Harwood, 1985) and may likely be associated with a lack of social stability in comparison to North Rona. It is therefore quite possible that the inland nature of the North Rona breeding site has promoted the possibility of sociality.

Behaviour of grey seal mothers has been shown to be related to environmental conditions in at least two examples. Grey seal mothers prefer breeding close to water and where this is not available they must spend more time in locomotion to water and necessarily less time with their pup. This has been shown both between different areas of the colony on the Isle of May and between a wet and atypically dry period on North Rona (Redman et al., 2001; Twiss et al., 2000). Increased locomotion in grey seals has been linked to increased rates of aggression (Redman, 2002) and is most likely linked to reduced social stability. In addition, Grey seal mothers breeding on ice in Nova Scotia were found to have a shorter lactation period and be more synchronous in pupping than their land-breeding counterparts (Haller et al., 1996). This was

thought to be in response to the reduced stability of ice as a substrate and so the increased risk of premature separation of mother and pup. It is therefore possible that the social behaviour displayed on North Rona is different to that displayed on other colonies and that the development of this behaviour may have been promoted in response to local environmental conditions.

#### 7.4 Sociality and genetics

Previous studies have failed to find any evidence of kin clustering within the North Rona colony. However, hotspots, associated with prime breeding areas, have been highlighted in which the individuals were more related to the colony as a whole than average (Pomeroy et al., 2001). Rather than illustrating a fine scale kin structure, this suggests that some mothers in some areas have disproportionately greater success in producing offspring that are then recruited into the colony than others. A more recent study has also found little evidence for kin clustering within the colony (Poland, 2005). It may seem likely that if cooperation were to develop, it would do so between close kin (Hamilton, 1964). However, there is also little evidence for reduced aggression between close relatives (Poland, 2005). Some evidence was provided for the clustering of females with higher genetic diversity (suggested to be positively correlated with individual fitness (Britten, 1996; Keller & Waller, 2002)) in areas of higher density and so possibly higher quality (Poland, 2005). This may also correlate with animals that experience high within year social stability. Further analysis is therefore needed to investigate the relationship between genetics and social behaviour.

Genetic studies have also provided evidence of mate fidelity operating within the grey seal population on North Rona (Amos et al., 1995). In addition, selection of genetically diverse mates occurs more than would be expected by chance and this provides a fitness benefit through increased pup survival (Amos et al., 2001; Bean et al., 2004). This suggests the possibility of kin recognition and possibly long term social recognition between the sexes.

Anecdotal evidence has been presented of a mother-daughter pair breeding together on North Rona (Pomeroy et al., 2000). Mother-pup associations appear the strongest of grey seal social bonds, although these are believed to be terminated at the time of weaning and so last only three weeks. It is possible that within this time the mother and pup may learn to recognise each other in a way that lasts after separation has occurred (Insley, 2000). If this is the case, or kin recognition allows individuals to distinguish relatives to any degree, then this initial familiarity may act to promote sociality between related individuals. Many animal societies are structured by female matrilineal groups (Gouzoules & Gouzoules, 1987; Summers & Tyack, 2000), a seemingly natural progression in extension of the early mother-offspring bond.

### 7.5 Sociality outwith the breeding season

Comparatively little is known of the lives of grey seals outwith the breeding season. However, if social organisation is present within breeding seasons (Chapter 5) then it is possible that such organisation extends into other periods of grey seal life history. Studies have used telemetry to investigate at sea behaviour and recent advances have allowed investigation of movement patterns, feeding grounds and habitat preferences (Matthiopoulos et al., 2004; McConnell

et al., 1999; Thompson et al., 1996). Due to the number of animals that would be required to be tracked and the spatial accuracy that would be necessary to infer association it has so far been beyond the scope of such studies to provide much insight into social behaviour. However, an attempt to track animals at sea on departure from the North Rona colony suggested the possibility of coordinated movement between individuals that were associated on land (Pomeroy, pers. comm.). Outwith the breeding season grey seals haul out between foraging trips and also more extensively every spring during the annual moult (Hewer, 1974). Large aggregations can form during such haul outs in which segregation of sex and age classes is common (pers. obs.). Photo-identification suggested that approximately 38% of the North Rona female breeding population attended the island outwith the breeding and moulting periods during the summer (Redman, 2002). However, it is perhaps more likely that as telemetry devices become smaller, cheaper and more diverse in function, that they will provide the next significant advances in understanding of year-round grey seal behaviour.

#### 7.6 Implications of sociality for animal behaviour

A prerequisite for social behaviour is individual recognition and in the grey seal this may be possible through olfactory, auditory or visual cues. Mothers sniff their pups shortly after birth and throughout lactation, presumably for the purpose of establishing identification (Burton et al., 1975; pers. obs.). Indeed, olfactory cues are often associated with kin recognition and in particular offspring are often recognised by scent (Mateo, 2002; Porter, 1999). Female grey seals are sometimes observed to sniff other females and males on initial

contact (pers. obs.). This is infrequent but may hint at a further role of this sense in social recognition.

Studies of individual recognition in pinnipeds have been predominantly focused on vocalisations. Grey seal mothers have been shown to recognise their own pup's vocalisations on Sable Island, Nova Scotia, but not on the Isle of May, Scotland (McCulloch et al., 1999; McCulloch & Boness, 2000). The vocal capabilities of grey seals are also quite flexible, a recent study demonstrating call usage learning in this species (Shapiro et al., 2004). Here individuals were capable of learning to vocalise in novel situations and distinguish between 9 unique vocalisations. However, they were not capable of generalising by call type. Many species of otariids, which generally have much extended periods of lactation in comparison to grey seals, are capable of long term vocal recognition between mother and pup (Dobson & Jouventin, 2003; Fern'Ndez-Juricic et al., 1999; Insley et al., 2003; Mathevon et al., 2004; Trillmich, 1981). The physical properties of sound appear to make it the most applicable for immediate communication through many media, be it water (Dudzinski et al., 2002) or a mass of individuals (Aubin et al., 2000; Trillmich, 1981), where olfactory or visual perception would be difficult.

The visual sense of the grey seal is adapted for their predominantly aquatic habit and they are myopic on land (Lavigne et al., 2001). Although visual discrimination has been shown in many animals (Parr et al., 2000; Ruiz-Miranda, 1992; Watanabe, 1992; Whitfield, 1986) it is unlikely that this sense plays a major role in grey seal individual recognition. However, the use of simple visual stimuli has been possible in some experimental settings (Hanggi & Schusterman, 1995; Kastelein et al., 1995). Grey seals are highly distinguishable

by their natural pelage markings (Hiby & Lovell, 1990) and visual identification would seem possible at least from the point of view of individual distinctiveness. It is likely that a combination of cues may be used for individual recognition, perhaps auditory at medium distances through groups of animals with reinforcement through olfactory cues on contact (Dobson & Jouventin, 2003). The extensive presence of mother-pup recognition in the pinnipeds does suggest that complex social interactions are possible (Insley et al., 2003) providing support, at least in principal, for the possibility of active social organisation.

### 7.7 Implications of sociality for population processes

This thesis has provided further insight into the life history of grey seals at the individual level. Much effort is put into monitoring this species on a population level through the SMRU's statutory obligation to provide assessment on the status of the UK population (SMRU, 2004). Individual behaviours are the building blocks of population processes and population dynamics can not be truly understood unless individual behaviour is characterised (Sutherland, 1996). If grey seals display social fidelity this has implications for immigration, emigration and for the rise and decline of local populations and breeding sites. In addition, combination of identification and genetic data may provide direct insight to the extent of inter-colony mixing (Chapter 6). Knowledge of individual behaviour is therefore invaluable for understanding population processes. Recent models of the UK grey seal population have highlighted the effect that different migratory behaviour can have on estimates of population dynamics (Matthiopoulos et al., 2005). If individuals are acting socially and not

as independent entities then this will have further implications for population modelling.

### 7.8 Success of methodology

The methodology developed in this thesis constitutes a novel approach to the description of sociality. It was developed specifically to measure change in the social environment to which animals are subject and thus provide an illustration of social dynamics within the colony. This is in contrast to measuring the presence or strength of individual pair-wise associations and inferring social structure using, for instance, network, sociogram or cluster analysis techniques (Whitehead & Dufault, 1999). The benefit of measuring social stability was that it addressed the specific hypothesis being proposed, that a more stable environment may be a better one in which to raise a pup. It was therefore more instructive than the description of presence or absence of individual associations. That is not to say the classical method of assessing pair-wise associations would not be of any use to studies of grey seal sociality. For instance, the strength of pair-wise associations between animals over a much longer series of breeding events, or at sea, may illustrate the strength of cohesion between individuals in a way that the measure of social stability can not. These two measures view sociality from slightly different angles but could be used in a complimentary way to provide a more detailed picture of sociality than is provided by using just one. This may be the case not only for systems presenting similar qualities to grey seal breeding colonies (for instance other pinniped breeding colonies), but also in the study of other systems that are traditionally described using only pair-wise measures (for instance those reviewed in Whitehead & Dufault (1999)). For

example, assessment of the social stability of cetacean pods, primate groups or ungulate herds may provide further insight into the social organisation of these animals.

Although instability in this study was hypothesised to be detrimental, it is instructive to think that in some systems a constant change of associates may be a benefit. Small world theory explains the high interconnectability of nodes (individuals) in social networks through a few highly connected super-nodes (Croft et al., 2004; Lusseau & Newman, 2004; Watts & Strogatz, 1998). It is not always clear, however, if being a super node is a good or a bad thing for the individual. If being a super-node requires having a multitude of associations it is likely that turnover of associates is high and so social stability low. Rather than super-nodes being seen as having lots of 'friends' they may actually be vagrants with little or no 'friends' but lots of changing associations. This may or may not be a benefit depending on context. For instance, sticklebacks (*Gasterosteus aculeatus*) are known to benefit from familiarity with other individuals (Utne-Palm & Hart, 2000). If being a super-node implies the inability for familiarity to be established then this may be a cost. However, in another system, being a super-node may be associated with maximal mating opportunity or information transfer for the location of resources and so may constitute a benefit. It is therefore instructive to examine social structure from a variety of angles, assessing the quantity, strength and change of associations.

The success of the methodology used in this study depends on the assumptions of how best to measure sociality for breeding female grey seals. Here, spatial proximity was used as a proxy for behavioural association (Whitehead & Dufault, 1999). But perhaps this does not encompass the real

biological relevance of associations on the colony. It is possible that only one or two pair-wise associations within the estimated association distance are actually relevant, be they nearest neighbours or otherwise. In addition, the temporal scale over which the study was conducted may not have been adequate to assess long term sociality. Although social behaviour was assessed on a variety of scales, from continuous observations to consecutive years, the study was limited to only two years. Perhaps the maintenance of associations and differences in social stability would be more obvious over a series of years. Assumptions were also required in the provision of null model simulations (Bejder et al., 1998; Whitehead, 1999). The main assumption that may be violated is the non-social credential of observed site fidelity. Such a violation would make the tests highly over conservative. Of course, the more evidence of sociality that these tests provide, the more conservative they appear!

### 7.9 Summary

A novel approach was constructed to assess sociality between breeding female grey seals on North Rona, Scotland. This approach overcomes the problems associated with measuring sociality on a pinniped breeding rookery and may have utility in the description of other social systems.

Detailed behavioural observations suggested that the spatial scale of association for breeding female grey seals was 10m within a season and 20m throughout a season. Simulations were constructed to test observed sociality against that expected due to observed spatial and temporal behaviour patterns. Both areas and individuals within the colony were found to be associated with both higher and lower within year social stability than would be expected by

chance suggesting at least some degree of active social organisation within the colony. In addition, areas of higher social stability were also those towards the centre of the colony with moderate access to pools and which were well populated with females at different stages of lactation. However, neither the assessment of between year social stability nor pair-wise re-associations provided conclusive evidence of active social organisation between breeding attempts. Although no relationship between social stability and aggression was found, a trend was evident for increased maternal efficiency with increased social stability within a breeding season. This suggests a possible fitness benefit of social organisation for this species.

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# APPENDIX A

The raw input data consists of individual identities and locations of animals identified during photographic surveys in a .csv format file with columns:

Data file

seal.no	individual identifier (1,2,3,4....)
x	full OSBG x coordinate
y	full OSBG y coordinate
time	- not used -
day	survey number (0,1,2,3...)

Function inputs:

A.1 "socarea"

file	data file
newfile	name of file to be created
sradius	distance over which social estimates are to be calculated (10m)

A.2 "socind"

file	data file
newfile	name of file to be created
sradius	distance over which social estimates are to be calculated (10m)

A.3 "unidentifieds"

datafile	data file
outputfile	name of file to be created
maxanimnumber	maximum identification number used in data file
searchradius	distance within which to reassign animals (10/20m)

A.4.1 "newsim possxy"

inputfile	data file
outputfile	name of file to be created

A.4.2 "distance.fn"

file	data file
newfile	name of file to be created

A.4.3 "newsim pdf"

inputfile	output file from "distance.fn"
nrecords	number of records (surveys) in distance file
output file	name of file to be created

A.4.4 "newsim fn9"

datafile	data file
possxyfile	output from "possxy.fn"
pdffile	output from "newsim_pdf.fn"
iterations	number of iterations to be simulated
itstartno	iteration number at which to start

A.4.5 "blanketavailabilityandmovementsim.fn9.fn" function for R  
inputs as above

## APPENDIX A.1 "socarea" function for R

```

function (file,newfile,sradius) {

## import file to be worked on
data<-read.table(file,sep=" ",header=T)

##### get all "SPOTS" coords to calc SS around #####
xs<-seq(181295,181365, by=10)
ys<-seq(1032625,1032715, by=10)
I<-length(xs)
J<-length(ys)
for(i in 1:I){ # start loop over xs
x<-xs[i]
for(j in 1:J){ # start loop over ys
y<-ys[j]
ifelse(i==1,
ifelse(j==1,spots<-data.frame(x,y),spots<-rbind(spots,c(x,y))),
spots<-rbind(spots,c(x,y)))
} # end loop over ys
} # end loop over xs
#####

S<-nrow(spots)
days<-max(data$day)
## create output matrices
output.a<-as.data.frame(matrix(NA,nrow=days+8,ncol=S+1))
output.b<-as.data.frame(matrix(NA,nrow=days+13,ncol=S+1))
output.c<-as.data.frame(matrix(NA,nrow=days+13,ncol=S+1))
output.D<-as.data.frame(matrix(NA,nrow=days+13,ncol=S+1))
output.J<-as.data.frame(matrix(NA,nrow=days+13,ncol=S+1))
output.S<-as.data.frame(matrix(NA,nrow=days+20,ncol=S+1))

for(s in 1:S){ # start loop over spots
## coords of current spot
x<-spots$x[s]
y<-spots$y[s]
## name of current spot
name<-paste("(",x,",",y,")",sep=" ")
## add name to names vector
ifelse(s==1,
names<-name,
names<-c(names,name))
## what spot are we on?
#print(paste("spot coords:",name))

##### delete all animals outwith sradius #####
temp.data<-data
seals<-nrow(temp.data)
for(seal in 1:seals){ # start loop over seals
## distance between current spot and current seal
xdiff<-abs(x-temp.data$x[seal])
ydiff<-abs(y-temp.data$y[seal])
dist<-sqrt(xdiff^2+ydiff^2)
##create distance vector
ifelse(seal==1,
distance<-dist,
distance<-c(distance,dist))
} # end loop over seals

temp.data<-cbind(temp.data,distance)
## remove those outwith sradius
temp.data<-temp.data[which(temp.data$distance<=sradius),]
## ! total number of animals around this spot over whole season to output = sum.s
!
output.a[24,s+1]<-nrow(temp.data)

## TOTAL NUMBER OF INDIVIDUALS AROUND THIS SPOT OVER WHOLE SEASON
individuals<-temp.data$seal.no
ifelse(length(individuals)!=0,lastindividual<-max(individuals),NA)

ifelse(length(individuals)!=0, #
for (individual in 1:lastindividual){ # start loop over individuals
ifelse(individual==1,
index<-which(individuals==individual)[1],
index<-c(index,which(individuals==individual)[1]))

```

## APPENDIX A

---

```

} # end loop over individuals
,NA) #
ifelse(length(individuals)!=0,
individuals<-which(individuals[index]!="NA")
,NA)
## write this to output ! S = number of individuals over whole season!
output.a[22,(s+1)]<-length(individuals)

## DAYTOTALS!
for (day in 0:days){ # start loop over days
## what day are we on?
#print(paste("day",day))
## what is the number of animals on this day
daytotal<-length(which(temp.data$day==day))
## write vector "daytotals" containing the totals for each day
ifelse(day==0, daytotals<-daytotal, daytotals<-c(daytotals,daytotal))
} # end loop over days

## number of days occupied:
days.occ<-length(which(daytotals!=0))
#print(paste("days.occ",days.occ))
output.a[23,s+1]<-days.occ
output.D[25,s+1]<-days.occ
output.J[25,s+1]<-days.occ
output.S[25,s+1]<-days.occ
## mean number of animals over all days
output.a[26,s+1]<-mean(daytotals)
## median number of animals over all days
output.a[25,s+1]<-median(daytotals)
## mean number of animals per day occupied
ifelse(sum(daytotals)!=0,output.a[28,s+1]<-sum(daytotals)/days.occ,
output.a[28,s+1]<-0)
## median number of animals per day occupied
ifelse(sum(daytotals)!=0,output.a[27,s+1]<-
median(daytotals[which(daytotals!=0)],na.rm=T), output.a[27,s+1]<-0)
## calculate H1
output.a[29,s+1]<-1-(((output.a[22,s+1]/output.a[26,s+1])-1)/(21))

##### do SS calcs #####
for (day in 1:days){ # start loop over days 2 (starts on day 1 as there is no SS
for day 0!
## who is there at day-1 = t1?
t1<-temp.data[which(temp.data$day==day-1),]
t1<-t1$seal.no
## who is there at day = t2?
t2<-temp.data[which(temp.data$day==day),]
t2<-t2$seal.no
## how many of these are the same from t1 to t2?
## concatenate t1 and t2
t1t2<-c(t1,t2)
## order t1t2
index<-order(t1t2)
t1t2<-t1t2[index]

same<-0
numbers<-length(t1t2)
ifelse(numbers!=0,
for (number in 1:numbers){ # start loopover numbers
ifelse(
((t1t2[number]+t1t2[number+1])/2)==t1t2[number],
same<-c(same,t1t2[number])
,NA)
} # end loop over numbers
,NA)
## get rid of 0 at start of same
same<-same[which(same!=0)]

a<-length(same)
b<-length(t1)-length(same)
c<-length(t2)-length(same)
output.a[day,s+1]<-a
output.b[day,s+1]<-b
output.c[day,s+1]<-c

} # end loop over days 2

## output.D = Dice coefficient = 2a / 2a+b+c

```

## APPENDIX A

```
output.D[1:21,s+1]<-(2*output.a[1:21,s+1]) / ((2*output.a[1:21,s+1]) +
output.b[1:21,s+1] + output.c[1:21,s+1]) # Dice for each timestep
output.D[22,s+1]<-mean(output.D[1:21,s+1],na.rm=T) # mean Dice (na.rm!)
output.D[23,s+1]<-median(output.D[1:21,s+1],na.rm=T) # median Dice (na.rm!)
output.D[24,s+1]<-(length(which(output.D[1:21,s+1]>=0)))/21 # proportion of time
steps for which a value is available

## output.J = Jaccard coefficient = a / a+b+c
output.J[1:21,s+1]<- output.a[1:21,s+1] / (output.a[1:21,s+1] +
output.b[1:21,s+1] + output.c[1:21,s+1]) # Jaccard for each time step
output.J[22,s+1]<-mean(output.J[1:21,s+1],na.rm=T) # mean Jaccard (na.rm!)
output.J[23,s+1]<-median(output.J[1:21,s+1],na.rm=T) # median Jaccard (na.rm!)
output.J[24,s+1]<-(length(which(output.J[1:21,s+1]>=0)))/21 # proportion of time
steps for which a value is available

## output.S = SC coefficient = a / a+b
output.S[1:21,s+1]<- output.a[1:21,s+1] / (output.a[1:21,s+1] +
output.b[1:21,s+1]) # SC for each timestep
output.S[22,s+1]<-mean(output.S[1:21,s+1],na.rm=T) # mean SC (na.rm!)
output.S[23,s+1]<-median(output.S[1:21,s+1],na.rm=T) # median SC (na.rm!)
output.S[24,s+1]<-(length(which(output.S[1:21,s+1]>=0)))/21 # proportion of time
steps for which a value is available

## other info
output.S[35,s+1]<-output.a[22,s+1]
output.S[36,s+1]<-output.a[24,s+1]
output.S[37,s+1]<-output.a[25,s+1]
output.S[38,s+1]<-output.a[26,s+1]
output.S[39,s+1]<-output.a[27,s+1]
output.S[40,s+1]<-output.a[28,s+1]
output.S[41,s+1]<-output.a[29,s+1]

} # end loop over spots

## make the first column of each array denote time step and extras
columnrefs<-
c("ts1", "ts2", "ts3", "ts4", "ts5", "ts6", "ts7", "ts8", "ts9", "ts10", "ts11", "ts12", "ts1
3", "ts14", "ts15", "ts16", "ts17", "ts18", "ts19", "ts20", "ts21")
output.a[,1]<-
c(columnrefs, "S", "days.occ", "sum.s", "median.s.all", "mean.s.all", "median.s.do", "me
an.s.do", "1-H1.all")
output.b[,1]<-
c(columnrefs, "mean", "median", "prop.expl", "days.occ", "1.mean", "1.median", "1.prop.e
xpl", "2.mean", "2.median", "2.prop.expl", "3.mean", "3.median", "3.prop.expl")
output.c[,1]<-
c(columnrefs, "mean", "median", "prop.expl", "days.occ", "1.mean", "1.median", "1.prop.e
xpl", "2.mean", "2.median", "2.prop.expl", "3.mean", "3.median", "3.prop.expl")
output.D[,1]<-
c(columnrefs, "mean", "median", "prop.expl", "days.occ", "1.mean", "1.median", "1.prop.e
xpl", "2.mean", "2.median", "2.prop.expl", "3.mean", "3.median", "3.prop.expl")
output.J[,1]<-
c(columnrefs, "mean", "median", "prop.expl", "days.occ", "1.mean", "1.median", "1.prop.e
xpl", "2.mean", "2.median", "2.prop.expl", "3.mean", "3.median", "3.prop.expl")
output.S[,1]<-
c(columnrefs, "mean", "median", "prop.expl", "days.occ", "1.mean", "1.median", "1.prop.e
xpl", "2.mean", "2.median", "2.prop.expl", "3.mean", "3.median", "3.prop.expl", "S", "sum
.s", "median.s.all", "mean.s.all", "median.s.do", "mean.s.do", "1-H1.all")
# note: 1.2.3.mean etc. denote headings for thirds but thirds output is not
# produced in this version!

## add coords to 1st row of each matrix
names<-c("coord",names)
names(output.a)<-names
names(output.b)<-names
names(output.c)<-names
names(output.D)<-names
names(output.J)<-names
names(output.S)<-names

save(list=c("output.a", "output.b", "output.c", "output.D", "output.J", "output.S"), fi
le=newfile)
}
```

APPENDIX A.2 "socind" function for R

```

function (file,newfile,sradius){

## import file to be worked on
data<-read.table(file,sep=" ",header=T)

##### get all "SPOTS" coords to calc SS around #####
xs<-seq(181295,181365, by=10)
ys<-seq(1032625,1032715, by=10)
I<-length(xs)
J<-length(ys)
for(i in 1:I){ # start loop over xs
x<-xs[i]
for(j in 1:J){ # start loop over ys
y<-ys[j]
ifelse(i==1,
ifelse(j==1,spots<-data.frame(x,y),spots<-rbind(spots,c(x,y))),
spots<-rbind(spots,c(x,y)))
} # end loop over ys
} # end loop over xs
#####

S<-nrow(spots)
days<-max(data$day)
## create output matrices
output.a<-as.data.frame(matrix(NA,nrow=days+8,ncol=S+1))
output.b<-as.data.frame(matrix(NA,nrow=days+13,ncol=S+1))
output.c<-as.data.frame(matrix(NA,nrow=days+13,ncol=S+1))
output.D<-as.data.frame(matrix(NA,nrow=days+13,ncol=S+1))
output.J<-as.data.frame(matrix(NA,nrow=days+13,ncol=S+1))
output.S<-as.data.frame(matrix(NA,nrow=days+20,ncol=S+1))

for(s in 1:S){ # start loop over spots

## coords of current spot
x<-spots$x[s]
y<-spots$y[s]
## name of current spot
name<-paste(" ",x," ",y," ",sep=" ")
## add name to names vector
ifelse(s==1,
names<-name,
names<-c(names,name))
## what spot are we on?
#print(paste("spot coords:",name))

##### delete all animals outwith sradius #####
temp.data<-data
seals<-nrow(temp.data)

for(seal in 1:seals){ # start loop over seals
## distance between current spot and current seal
xdiff<-abs(x-temp.data$x[seal])
ydiff<-abs(y-temp.data$y[seal])
dist<-sqrt(xdiff^2+ydiff^2)
##create distance vector
ifelse(seal==1,
distance<-dist,
distance<-c(distance,dist))
} # end loop over seals

temp.data<-cbind(temp.data,distance)
## remove those outwith sradius
temp.data<-temp.data[which(temp.data$distance<=sradius),]
## ! total number of animals around this spot over whole season to output = sum.s
!
output.a[24,s+1]<-nrow(temp.data)

## TOTAL NUMBER OF INDIVIDUALS AROUND THIS SPOT OVER WHOLE SEASON
individuals<-temp.data$seal.no
ifelse(length(individuals)!=0,lastindividual<-max(individuals),NA)
ifelse(length(individuals)!=0, #
for (individual in 1:lastindividual){ # start loop over individuals
ifelse(individual==1,
index<-which(individuals==individual)[1],

```

```

index<-c(index,which(individuals==individual)[1]))
) # end loop over individuals
,NA) #
ifelse(length(individuals)!=0,
individuals<-which(individuals[index]!="NA")
,NA)
## write this to output ! S = number of individuals over whole season!
output.a[22,(s+1)]<-length(individuals)

## DAYTOTALS!
for (day in 0:days){ # start loop over days
## what day are we on?
#print(paste("day",day))
## what is the number of animals on this day
daytotal<-length(which(temp.data$day==day))
## write vector "daytotals" containing the totals for each day
ifelse(day==0, daytotals<-daytotal, daytotals<-c(daytotals,daytotal))
} # end loop over days

## number of days occupied:
days.occ<-length(which(daytotals!=0))
output.a[23,s+1]<-days.occ
output.D[25,s+1]<-days.occ
output.J[25,s+1]<-days.occ
output.S[25,s+1]<-days.occ
## mean number of animals over all days
output.a[26,s+1]<-mean(daytotals)
## median number of animals over all days
output.a[25,s+1]<-median(daytotals)
## mean number of animals per day occupied
ifelse(sum(daytotals)!=0,output.a[28,s+1]<-sum(daytotals)/days.occ,
output.a[28,s+1]<-0)
## median number of animals per day occupied
ifelse(sum(daytotals)!=0,output.a[27,s+1]<-
median(daytotals[which(daytotals!=0)],na.rm=T), output.a[27,s+1]<-0)
## calculate H1
output.a[29,s+1]<-1-(((output.a[22,s+1]/output.a[26,s+1])-1)/(21))

##### do SS calcs #####
for (day in 1:days){ # start loop over days 2 (starts on day 1 as there is no SS
for day 0!
## who is there at day-1 = t1?
t1<-temp.data[which(temp.data$day==day-1),]
t1<-t1$seal.no
## who is there at day = t2?
t2<-temp.data[which(temp.data$day==day),]
t2<-t2$seal.no
## how many of these are the same from t1 to t2?
## concatenate t1 and t2
t1t2<-c(t1,t2)
## order t1t2
index<-order(t1t2)
t1t2<-t1t2[index]

same<-0
numbers<-length(t1t2)
ifelse(numbers!=0,
for (number in 1:numbers){ # start loopover numbers
ifelse(
((t1t2[number]+t1t2[number+1])/2)==t1t2[number],
same<-c(same,t1t2[number])
,NA)
} # end loop over numbers
,NA)
## get rid of 0 at start of same
same<-same[which(same!=0)]

a<-length(same)
b<-length(t1)-length(same)
c<-length(t2)-length(same)
output.a[day,s+1]<-a
output.b[day,s+1]<-b
output.c[day,s+1]<-c

} # end loop over days 2

## output.D = Dice coefficient = 2a / 2a+b+c

```

## APPENDIX A

```

output.D[1:21,s+1]<-(2*output.a[1:21,s+1]) / ((2*output.a[1:21,s+1]) +
output.b[1:21,s+1] + output.c[1:21,s+1]) # Dice for each timestep
output.D[22,s+1]<-mean(output.D[1:21,s+1],na.rm=T) # mean Dice (na.rm!)
output.D[23,s+1]<-median(output.D[1:21,s+1],na.rm=T) # median Dice (na.rm!)
output.D[24,s+1]<-(length(which(output.D[1:21,s+1]>=0)))/21 # proportion of time
steps for which a value is available

## output.J = Jaccard coefficient = a / a+b+c
output.J[1:21,s+1]<- output.a[1:21,s+1] / (output.a[1:21,s+1] +
output.b[1:21,s+1] + output.c[1:21,s+1]) # Jaccard for each time step
output.J[22,s+1]<-mean(output.J[1:21,s+1],na.rm=T) # mean Jaccard (na.rm!)
output.J[23,s+1]<-median(output.J[1:21,s+1],na.rm=T) # median Jaccard (na.rm!)
output.J[24,s+1]<-(length(which(output.J[1:21,s+1]>=0)))/21 # proportion of time
steps for which a value is available

## output.S = SC coefficient = a / a+b
output.S[1:21,s+1]<- output.a[1:21,s+1] / (output.a[1:21,s+1] +
output.b[1:21,s+1]) # SC for each timestep
output.S[22,s+1]<-mean(output.S[1:21,s+1],na.rm=T) # mean SC (na.rm!)
output.S[23,s+1]<-median(output.S[1:21,s+1],na.rm=T) # median SC (na.rm!)
output.S[24,s+1]<-(length(which(output.S[1:21,s+1]>=0)))/21 # proportion of time
steps for which a value is available

## other info
output.S[35,s+1]<-output.a[22,s+1]
output.S[36,s+1]<-output.a[24,s+1]
output.S[37,s+1]<-output.a[25,s+1]
output.S[38,s+1]<-output.a[26,s+1]
output.S[39,s+1]<-output.a[27,s+1]
output.S[40,s+1]<-output.a[28,s+1]
output.S[41,s+1]<-output.a[29,s+1]

) # end loop over spots

## make the first column of each array denote time step and extras
columnrefs<-
c("ts1", "ts2", "ts3", "ts4", "ts5", "ts6", "ts7", "ts8", "ts9", "ts10", "ts11", "ts12", "ts1
3", "ts14", "ts15", "ts16", "ts17", "ts18", "ts19", "ts20", "ts21")
output.a[,1]<-
c(columnrefs, "S", "days.occ", "sum.s", "median.s.all", "mean.s.all", "median.s.do", "me
an.s.do", "1-H1.all")
output.b[,1]<-
c(columnrefs, "mean", "median", "prop.expl", "days.occ", "1.mean", "1.median", "1.prop.e
xpl", "2.mean", "2.median", "2.prop.expl", "3.mean", "3.median", "3.prop.expl")
output.c[,1]<-
c(columnrefs, "mean", "median", "prop.expl", "days.occ", "1.mean", "1.median", "1.prop.e
xpl", "2.mean", "2.median", "2.prop.expl", "3.mean", "3.median", "3.prop.expl")
output.D[,1]<-
c(columnrefs, "mean", "median", "prop.expl", "days.occ", "1.mean", "1.median", "1.prop.e
xpl", "2.mean", "2.median", "2.prop.expl", "3.mean", "3.median", "3.prop.expl")
output.J[,1]<-
c(columnrefs, "mean", "median", "prop.expl", "days.occ", "1.mean", "1.median", "1.prop.e
xpl", "2.mean", "2.median", "2.prop.expl", "3.mean", "3.median", "3.prop.expl")
output.S[,1]<-
c(columnrefs, "mean", "median", "prop.expl", "days.occ", "1.mean", "1.median", "1.prop.e
xpl", "2.mean", "2.median", "2.prop.expl", "3.mean", "3.median", "3.prop.expl", "S", "sum
.s", "median.s.all", "mean.s.all", "median.s.do", "mean.s.do", "1-H1.all")
# note: 1.2.3.mean etc denotes thirds - not outputted in this version!

## add coords to 1st row of each matrix
names<-c("coord",names)
names(output.a)<-names
names(output.b)<-names
names(output.c)<-names
names(output.D)<-names
names(output.J)<-names
names(output.S)<-names

save(list=c("output.a", "output.b", "output.c", "output.D", "output.J", "output.S"), fi
le=newfile)
}

```

APPENDIX A.3 "unidentifieds" function for R

```

function (datafile,outputfile,maxanimnumber,searchradius){
# maxanimnumber = largest animal number in ID'd sample - so new ids
# are assigned as maxanimnumber+1 and over

data<-read.table(datafile,sep=" ",header=T)
unidindex<-which(data$unid==1)
for (unid in unidindex){ # start loop over unidentifieds

## create temp.data to work from
temp.data<-data
if(unid==c(31)){print(temp.data[unid,])}

## animals present at day-1 and day+1
temp.data<-temp.data[which(which(temp.data[,5]==data[unid,5]-
1|temp.data[,5]==data[unid,5]+1),),]
if(unid==c(31)){print(temp.data)}

## remove other unids from list
temp.data<-temp.data[which(temp.data$unid==0),]
if(unid==c(31)){print(temp.data)}

## list of animals other than present unid present at day of unid
temp.daylist<-data[which(data$day==data$day[unid]),1]
if(unid==c(31)){print(temp.daylist)}

## remove animals from temp.data that are present on the same day as unid
alreadythere<-NULL
for(i in 1:length(temp.daylist)){ # start loop over i in temp.daylist
for(j in 1:nrow(temp.data)){ # start loop over j in temp.data
if(temp.daylist[i]==temp.data[j,1]){alreadythere<-c(alreadythere,j)}
} # end loop over i
} # end loop over j
if(unid==c(31)){print(alreadythere)}
temp.data<-temp.data[-alreadythere,]
if(unid==c(31)){print(temp.data)}

## distance between these and current unid to time column?
temp.data$time<-sqrt(((abs(data[unid,2]-temp.data$x)^2)+((abs(data[unid,3]-
temp.data$y))^2))
if(unid==c(31)){print(temp.data)}

## delete those outwith 10m radius
temp.data<-temp.data[which(temp.data$time<=searchradius),]
if(unid==c(31)){print(temp.data)}

## if there are any potentials left, assign at random, otherwise assign a new id
ifelse(nrow(temp.data)>0,data[unid,1]<-
temp.data[runif(1,1,nrow(temp.data)),1],data[unid,1]<-maxanimnumber+1)
## if id assigned from p[otentials denote as "2" else denote as "3"
ifelse(nrow(temp.data)>0,data[unid,6]<-2,data[unid,6]<-3)
## if id assigned as new, increase maxanimnumber by 1
if(nrow(temp.data)==0){maxanimnumber<-maxanimnumber+1}

} # end loop over unidentifieds
## save output
write.table(data,file=outputfile,sep=" ",row.names=F)}

```

APPENDIX A.4.1 "newsim possxy.fn" function for R

```
function (inputfile,outputfile){  
  
## read in file to turn into possxy file  
data<-read.table(inputfile,,sep=" ",header=T)  
  
## what is the length of that file?  
print(paste("number of records in input file:",nrow(data)))  
## what is the number of unique x,y entries  
print(paste("number of unique x,ys in input file:",nrow(unique(data[,2:3]))))  
  
## create dist and weight vectors  
dist<-rep(NA,nrow(data))  
weight<-rep(0,nrow(data))  
  
## create output file  
possxy<-data.frame(data[,2],data[,3],dist,weight)  
print(possxy[1:5,])  
  
## create column names for output file  
names<-c("x","y","dist","weight")  
names(possxy)<-names  
print(possxy[1:5,])  
  
## save output file  
write.table(possxy,file=outputfile,row.names=F,sep=" ")  
}
```

APPENDIX A.4.2 "distance" function for R

```

function (file, newfile){

## import file to be worked on
data<-read.table(file,sep=" ",header=T)
seals<-max(data$seal.no)
## note: seals must be numbered sequentially starting at 1!

for(seal in 1:seals){ # start loop over seals
## what seal are we on?
print(paste("seal",seal))

days<-max(data$day)

## if on first seal create distance data frame else add to it
day<-seq(1:days)
day<-
c(day,"days.present","dist.mean","dist.median","dist.var","max.displ","no.first",
"no.last","dist2.mean","dist2.median","dist2.var","max.displ.nfl")
a<-rep(NA,days+11)
ifelse(seal==1,
distance<-data.frame(day,a),
distance<-data.frame(distance,a))

## just this seal
temp.data<-data[which(data$seal.no==seal),]

## max displacement over whole season if more than one data point
if(nrow(temp.data)>=2){
maxx<-max(temp.data$x)
minx<-min(temp.data$x)
maxy<-max(temp.data$y)
miny<-min(temp.data$y)
xdiff<-abs(maxx-minx)
ydiff<-abs(maxy-miny)
maxdispl<-sqrt(xdiff^2+ydiff^2)

## write to output
distance[days+5,seal+1]<-maxdispl

## days where seal is present
present<-data$day[which(data$seal.no==seal)]
print("present:")
print(present)
## write to output
distance[days+1,seal+1]<-length(present)

## days where seal is present at t1 and t2 <- present2
present2<-numeric(0)
for(p in present){
pindex<-which(present==p)
ifelse(p-1==present[pindex-1],present2<-c(present2,p),NA)}
print("present2:")
print(present2)

for (day in present2){ # start loop over days present
#print(paste("day",day))
x1<-temp.data$x[which(temp.data$day==day-1)]
y1<-temp.data$y[which(temp.data$day==day-1)]
x2<-temp.data$x[which(temp.data$day==day)]
y2<-temp.data$y[which(temp.data$day==day)]
xdiff<-abs(x1-x2)
ydiff<-abs(y1-y2)
dist<-sqrt(xdiff^2+ydiff^2)
#print(dist)

## write to output
distance[day,seal+1]<-dist

} # end loop over days present2

distance[(days+2),(seal+1)]<-mean(distance[1:days,(seal+1)], na.rm=TRUE)
distance[(days+3),(seal+1)]<-median(distance[1:days,(seal+1)], na.rm=TRUE)
distance[(days+4),(seal+1)]<-var(distance[1:days,(seal+1)], na.rm=TRUE)

```

```

distance2<-distance[1:days, (seal+1)]
distance2<-distance2[which(distance2!="NA")]
print(distance2)
distance2b<-numeric(0)

distance[days+6,seal+1]<-0
distance[days+7,seal+1]<-0

## if first/last movement is 3*the mean movement(nfl) then remove it

if(length(distance2)>=3){

## create distance2 no first last
distance2nf<-distance2[-1]
distance2nfl<-distance2nf[-length(distance2nf)]
print(distance2nfl)

## mean of distance2 no first last
meannfl<-mean(distance2nfl)
print(meannfl)

if(distance2[1]>=3*meannfl){
distance2<-distance2[-1]
distance[days+6,seal+1]<-1
}

if(distance2[length(distance2)]>=3*meannfl){
distance2<-distance2[-length(distance2)]
distance[days+7,seal+1]<-1
}
}

## new descriptives
if(length(distance2)!=0){distance[days+8,seal+1]<-mean(distance2, na.rm=T)}
if(length(distance2)!=0){distance[days+9,seal+1]<-median(distance2, na.rm=T)}
if(length(distance2)!=0){distance[days+10,seal+1]<-var(distance2, na.rm=T)}

## max.displ.nfl (if more than 1 data point)- note difference between ##
first/last movement measurements and first/last coords!
temp.data<-temp.data[-1,]
if(nrow(temp.data)>=2){temp.data<-temp.data[-nrow(temp.data),]}
if(nrow(temp.data)>=2){
maxx<-max(temp.data$x)
minx<-min(temp.data$x)
maxy<-max(temp.data$y)
miny<-min(temp.data$y)
xdiff<-abs(maxx-minx)
ydiff<-abs(maxy-miny)
maxdispl<-sqrt(xdiff^2+ydiff^2)
distance[days+11,seal+1]<-maxdispl}

} # end loop over seals

## create a vector of row names
names<-c("day",paste("seal",c(1:seals),sep=" "))
## rename distance data frame with row names
names(distance)<-names

columns<-c(1,2,3,4,5,27,40,58)
print(distance[columns])

## write to file called newfile
write.table(distance,file=newfile,row.names=F,sep=" ")
}

```

APPENDIX A.4.3 "newsim\_pdf.fn" function for R

```
function (inputfile,nrecords,outputfile) {  
  ## read in input file  
  data<-read.table(inputfile,sep=" ",header=T)  
  #print(data[,1:5])  
  
  ## chop out statistics at bottom and day column  
  data<-data[1:nrecords,2:length(data[1,])]  
  #print(data[,1:5])  
  
  ## turn data frame into 1 long vector  
  data<-stack(data)[,1]  
  ## remove NAs  
  data<-data[which(data!="NA")]  
  print(data[1:10])  
  print(summary(data))  
  hist(data,prob=T)  
  
  ## create outputfile  
  dist<-seq(0,300)  
  prob<-rep(0,301)  
  pdf<-data.frame(dist,prob)  
  #print(pdf[1:5,])  
  
  ## add 1 to prob vector for every occurrence of a distance  
  for(i in 1:length(data)){  
    pdf[data[i]+1,2]<-pdf[data[i]+1,2]+1  
  }  
  print(pdf[1:5,])  
  
  ## convert numbers in prob vector from counts to probs  
  pdf$prob<-pdf$prob/sum(pdf$prob)  
  print(pdf[1:5,])  
  
  print(sum(pdf$prob))  
  plot(pdf$dist,pdf$prob,type="l")  
  
  ## save to output  
  write.table(pdf,file=outputfile,row.names=F,sep=" ")  
}
```

## APPENDIX A.4.4 "newsim.fn" function for R

```

function (datafile,possxyfile,pdffile,iterations,itstartno){

for(iteration in 1: iterations){
data<-read.table(datafile,sep=" ",header=T)
possxy<-read.table(possxyfile,sep=" ",header=T)
pdf<-read.table(pdffile,sep=" ",header=T)
## for every record in data where day > 0
day1<-nrow(data[which(data$day==0),])+1
nrecords<-nrow(data)

for (r in day1:nrecords){ # start loop over records

## what record are we on?
print(paste("record #",r))
## what is the current day?
cday<-data$day[r]
## what is current id?
cid<-data$seal.no[r]
## create temp possxy to work from
tempossxy<-possxy

## what coords have already been assigned today?
a<-data[day1:r-1,][which(data[day1:r-1,]$day==cday),]
p<-nrow(a)
if(p>0){
for(q in 1:p){
## delete this coordinate from tempossxy
tempossxy<-tempossxy[- which(tempossxy$x==a[q,2]&tempossxy$y==a[q,3]) ,]
}}

## find coords of current id when it was last seen
b<-data[which(data[1:r-1,]$seal.no==cid),]
b<-b[nrow(b),]

## if current id has not been seen before (ie. b is of 0 rows)
## assign a new coord randomly from tempossxy which has repetition
## of locations used more than once
if(nrow(b)==0){data[r,2:3]<-tempossxy[runif(1,1,nrow(tempossxy)),1:2]}

## if current id has been seen before (ie. b is of 1 row) then
## assign a new coord from tempossxy weighted by probs from pdf
## divided by the number of available locations at that distance
if(nrow(b)==1){
## find distance between previous xy (in b) and all tempossxys
## and then round down (floor) to 1m bins
tempossxy$dist<-sqrt(abs(tempossxy$x-b$x)^2+abs(tempossxy$y-b$y)^2)
tempossxy$dist<-floor(tempossxy$dist)
## count number of available locations in 1m bins
## create tempossxy2
tempossxy2<-tempossxy
## aggregate tempossxy by distance
tempossxy2<-aggregate(tempossxy2$dist,by=list(tempossxy2$dist),FUN=length)
## aggregate creates Group.1 as a factor with levels -
## the following reverts to numeric so the vector can be used as an index
tempossxy2$Group.1<-as.numeric(levels(tempossxy2$Group.1))[tempossxy2$Group.1]
## create pdf2 with probabilities divided by availability from tempossxy2
pdf2<-pdf
pdf2$prob[tempossxy2[,1]+1]<-pdf2$prob[tempossxy2[,1]+1]/tempossxy2[,2]
## assign weight in tempossxy by prob for moving that distance / availability
## of locations at that distance according to pdf2
tempossxy$weight<-pdf2$prob[tempossxy$dist+1]
## assign a new coordinate randomly (weighted) from tempossxy
data[r,2:3]<-tempossxy[sample(nrow(tempossxy),1,prob=tempossxy$weight),1:2]
}
} # end loop over records

## write to file
citation<-(itstartno-1)+iteration
newfile<-paste("sim",citation,".csv",sep=" ")
write.table(data,file=newfile,row.names=F,sep=" ")
}
}

```

APPENDIX A.4.5 "blanketavailabilityandmovementsim.fn9.fn" function for R

```

function (datafile,possxyfile,iterations,itstartno)
{
  for(iteration in 1: iterations){

data<-read.table(datafile,sep=" ",header=T)
possxy<-read.table(possxyfile,sep=" ",header=T)
#print("start data")
#print(data)
print("start possxy")
print(possxy)

## for every record in data where day > 0
day1<-nrow(data[which(data$day==0),])+1
nrecords<-nrow(data)

#####
for (r in day1:nrecords){ # start loop over records
#####

## what record are we on?
print(paste("record #",r))

## what is the current day?
cday<-data$day[r]

## what is current id?
cid<-data$seal.no[r]

## create temp possxy to work from
tempossxy<-possxy
#print(tempossxy)

## what coords have already been assigned today?
a<-data[day1:r-1,][which(data[day1:r-1,]$day==cday),]
#print(a)
## loop over records in a to remove them from tempossxy
p<-nrow(a)
if(p>0){
for(q in 1:p){
## delete this coordinate from tempossxy
tempossxy<-tempossxy[- which(tempossxy$x==a[q,2]&tempossxy$y==a[q,3]) ,]
}}

#print(tempossxy)

## assign a new coord randomly from tempossxy which has repetition
## of locations used more than once
{data[r,2:3]<-tempossxy[runif(1,1,nrow(tempossxy)),1:2]}
#print(data)

###
} # end loop over records
###

print(iteration)
print("end data")
print(data)

## write to file
citeration<-(itstartno-1)+iteration
newfile<-paste("Blanketavailabilityandmovement_sim",citeration,".csv",sep="")
write.table(data,file=newfile,row.names=F,sep=" ")
}
}

```

# APPENDIX B

# Breeding site choice fails to explain interannual associations of female grey seals

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**Abstract** Consistent, widespread fine-scale preferences for breeding sites may favour the emergence of intrasexual associations and hence sociality. Pairwise association was defined for a terrestrially breeding phocid seal in which intraseasonal colony mixing is limited and mothers spend only 3 weeks ashore breeding. Interannual associations may occur between pairs of breeding female grey seals at North Rona, Scotland because of pupping site fidelity, 90% return rates and limited variability in parturition dates that individual mothers show. Associations can occur when mothers are found together irrespective of location, or because of joint preferences for locations. Mothers were sedentary and were unlikely to interact if they are separated by >20 m. Using spatial and temporal association criteria, 160 of 176 of known mothers had intraseasonal associations with at least one other mother, with 14 of 126 (11.1%) of associations repeated in 2 years. The likelihood of female association in 2 years as a result of site fidelity, parturition date variation and pupping site quality was modelled. Interannual association between mothers that changed their pupping sites by up to the median observed pupping site fidelity (<40 m) was indistinguishable from our model's predictions. However, the number of mothers that showed interannual association after displacements of >40 m from their previous year's pupping sites was almost five times greater than the model predicted. We conclude that active association between adult female grey seals is not determined solely by habitat preference, and argue that examination of simple sociality in temporarily aggregating species can contribute significantly to socioecological models of social evolution.

**Keywords** Interannual spatial association - Intra-annual spatial association - Pupping site fidelity - Parturition date variability

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## Introduction

Population social structure is the result of spatially varying interactions between individuals that arise from constraints imposed by physical landscape, life-history and behaviour, resulting in non-random associations between individuals. Even if established by passive means, these non-random associations set the social context in which behavioural mechanisms of sociality can evolve (Axelrod and Hamilton *1981*; Michod and Sanderson *1985*; Ferriere and Michod *1996*). Large groups of animals often occur where resources such as nesting sites, overwintering sites or feeding areas have a patchy distribution, and where large groups provide protection from predators (Alcock *1993*; Krebs and Davies *1995*). Within these groups, non-random associations—which occur because animals spend long periods of time in close proximity—may generate “reciprocity in behaviour”, which in turn reinforces bonds between animals and leads to active association and conflict reduction (Michod *1999*). Therefore formation of groups where associations can occur is seen as a prerequisite in the evolution of sociality (Michod *1999*).

The nature of interactions between individuals are indicators of higher levels of social organisation typified by cooperation and reciprocal altruism (Hinde *1976*) and consequently the existence and identity of allies/associates can be determined by examining behaviours between group members, such as the incidences of allogrooming between individuals (e.g. Sugiyama *1988*; Dobson et al. *1998*). Cooperative breeding occurs in only 3% of bird and mammal species (Newton *1989*; Emlen *1997*). Simpler forms of sociality, such as conflict reduction, are likely to be prevalent, if not ubiquitous, where non-random associations between individuals occur. Unfortunately, conflict reduction is much more difficult to measure, especially when animals have few interactions with each other. Further, empirical evidence is difficult to obtain from animals that are difficult to observe, such as most marine mammals and nocturnal species. Even when all animals in a group can be identified individually it may be impossible to observe all interactions between them and alternative means of defining association have been used (reviewed in Whitehead and Dufault *1999*). A useful proxy is to classify animals by group membership or proximity. The assumption here is that spatial association is necessary before behavioural association can occur. It is important that the scale of spatial association is defined for a study species, as species-specific traits such as their methods of communication, the size of their home range and the medium in which they live will determine the range over which spatial association may be

present. Therefore animals classified as associates may be separated by anything from 1 or 2 m (e.g. greater white-toothed shrew, Cantoni and Vogel *1989*; captive Japanese macaques, Corradino *1990*) to 100 m or more (e.g. giraffes, Leuthold *1979*; coyote, Andelt *1985*; white tailed mongoose, Waser and Waser *1985*). Measures of association based on proximity may also vary contextually. Arnold et al. (*1981*), classed individual resting sheep as associated if they were within an area of 50 m<sup>2</sup>, but sheep grazing within an area of 400 m<sup>2</sup> were also considered as associated.

Detection and description of associations in most species have involved animals that are habitually gregarious or live in fission–fusion societies. We address the question of whether long-term associations occur in species which aggregate temporarily. Previous studies showed that in a long-lived polygynous mammal, the grey seal, adult females display a high degree of site fidelity to previous pupping locations (<55 m at North Rona and the Isle of May, Pomeroy et al. *1994, 2000a*), have high fecundity rates and give birth on or around the same date each year (Pomeroy et al. *1994, 2001*). It is likely therefore that mothers can come into contact with the same individuals in consecutive breeding episodes, satisfying the first criteria for potential social structure through non-random association (Michod *1999*). However, it is not known whether associations between female grey seals actually exist at a spatial scale that will affect their behaviour. Mothers on North Rona (NR) tend to remain close to their pups (e.g. Anderson et al. *1975*) and preliminary observations on a small subsample of mothers suggested that they moved less than 10 m within a day (Aust and Pomeroy, unpublished). In addition, overt interactions tend to occur only between mothers that come within 3–4 m of one another (Redman *2002*). Therefore it may be hypothesised that associations on breeding colonies would occur on a very local scale, perhaps between nearest neighbours. Nevertheless, mothers can travel between their pups and the nearest available water and this movement may bring them into contact with mothers outside their immediate pupping vicinity (Kovacs *1987*; Redman et al. *2001*). This may result in interactions between mothers over a greater area than would at first be expected. Any definition of spatial association for these animals must therefore take into consideration daily movements that bring individuals close enough to one another that they are likely to interact. The likelihood of occurrence of associations within the observed behavioural patterns may then be evaluated for seals within the colony.

The aims of this work were to (1) derive appropriate measures of spatial and temporal association for breeding female grey seals, (2) measure the frequency and extent of intra- and interannual association on NR using the locations of known mothers in successive breeding seasons, (3) model the probability of association between mothers in successive breeding seasons on NR, (4) compare the model's predictions with observed behaviour of known mothers. The null hypothesis for this work was that reoccurrences of neighbours in space and time on the NR grey seal

breeding colony could be explained solely by a model including site fidelity, parturition date variability and breeding site preference.

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## Methods

North Rona ( $59^{\circ}06'N$ ,  $05^{\circ}50'W$ ) lies about 75 km north-north-west of Cape Wrath, Scotland. The uninhabited island covers an area of  $1.2 \text{ km}^2$ , rising to 108 m above sea level. Most seals breed on the relatively low-lying northern peninsula of Fianuis (Boyd et al. *1962*). This work's study area (SA), lies at the southern end of Fianuis, covering an area of  $0.38 \text{ km}^2$ . A few narrow gullies on the east side of Fianuis give seals access from the sea to an open, boulder-strewn grassy slope.

The pupping season on NR spans late September to late November (Boyd and Laws *1962*). The peak in pupping occurs around the 8th of October (Hiby et al. *1996*). Initially, pregnant females on NR aggregate around pools of water and access gullies. Subsequently seals spread up to 300 m inland to pup, normally remaining close to their pups throughout lactation (Anderson et al. *1975*; Pomeroy et al. *1994*). The colony has been present on NR since at least 1844 (Boyd et al. *1962*) and pup production is currently stable, with approximately 1,100 pups born in 2000 (Duck *2003*).

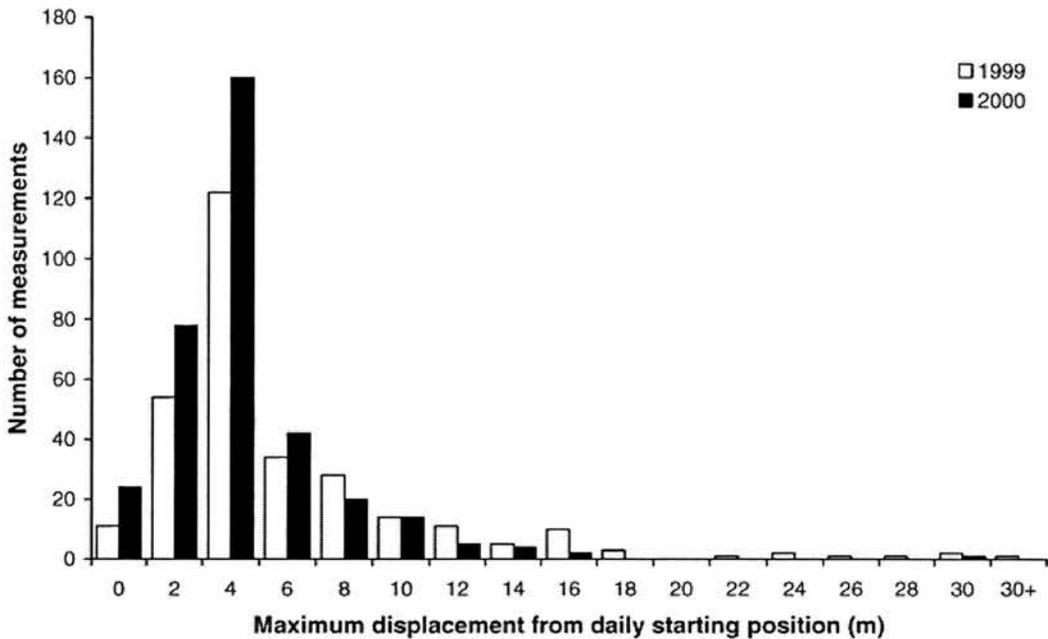
Groups of mothers and their pups were observed at predefined places within the SA on NR in the 1998–2000 breeding seasons. Each observation area was delineated using permanent landmarks and covered approximately  $20 \text{ m} \times 20 \text{ m}$ . Most seals within an observation area were identified by their natural pelage markings (Redman *2002*), but in a few cases by previously applied tags or brands (Fedak and Anderson *1982*). Briefly, images of individual female pelage patterns were collected as: (1) sketches on prepared outline sheets; (2) video images, or (3) black and white 35-mm photographs. Digital video images allowed post-hoc checking of sketch details in the field. A female whose pelage image was recorded is referred to subsequently as a “known” female. Seals became part of the focal group (study animals) if they entered one of the predefined observation areas, but known animals also occurred elsewhere. Daily focal group size ranged from 3 to 20 mothers, plus their pups and any males in the immediate vicinity. Groups were observed at a range of approximately 150 m, from a hide on a ridge overlooking the SA.

Continuous observations were made using binoculars during daylight hours. The first hour of each observation period was used to check all visible females for known individuals. Once detected, locations and ages of pups were recorded for known females. Subsequently, study animals' locations were plotted hourly on A4 transparency sheets superimposed on high resolution maps of the observation areas overlaid with a  $2 \text{ m} \times 2 \text{ m}$  grid, allowing accurate positioning (within 2 m) of the animals within the

SA. These maps were derived from aerial photographs which were digitised and geo-rectified using a geographical information systems (GIS) database (ArcInfo Version 8.3, Environmental Systems Research Institute, ESRI, Redlands, California; Twiss et al. *2000a*, *2000b*). Locations of known mothers and study mothers were also mapped on days when full behavioural observations were not made.

## **Classifying intra-annual spatial association for grey seal mothers on North Rona**

Each mother's displacement from her daily starting location was calculated at hourly intervals as the Euclidian distance between start and finish  $x, y$  coordinates. Only mothers with pups were included, as pregnant and non-parous females do not have the same movement constraints as lactating females. Animals that had poor images of their pelage markings and were therefore difficult or less likely to resight were also not used in the association analysis. The spatial scale at which associations are meaningful was investigated by recording the maximum displacement from the starting location for each female on each day the female was observed. Hourly locations were recorded in 1998, 1999 and 2000, but in 1998 daily movement was affected by the unusually limited availability of pools during the start of the season. Some mothers travelled more than 100 m from their pups to gain access to water, with no end point recognizable (Redman et al. *2001*), therefore only data from 1999 and 2000 (650 measurements) were used for the analysis of daily movement. In 1999 and 2000 respectively, 88% and 97% of measurements involved a maximum displacement from the daily starting position of <10 m (Fig. 1). Therefore mothers separated by more than 20 m were unlikely to interact and a separation distance of 20 m was used as the threshold distance within which associations might occur. A single location was identified for each mother representing the maximum use position during her time ashore. This was estimated as the centre of the 99.9% circular kernel estimator contour for all her recorded positions, using the PointDensity command and circular kernel estimators in ArcInfo (ESRI). These centers are referred to hereafter as LOCs (location centres). Mothers were defined as associated within a breeding season if they satisfied two conditions; (1) LOCs were within 20 m of one another and (2) they had pupping dates within 9 days of each other. This classification ensures that mothers were temporally as well as spatially associated and only considered animals for which detailed pupping information was available.



**Fig. 1** Maximum displacement from the starting position on each day for mothers on North Rona 1999 and 2000 ( $n=149$  subjects, 650 measures)

## Measuring interannual spatial association between female grey seals on the breeding colony

In each year, daily locations of all known females were converted into a single ArcInfo (ESRI) GIS point coverage which was incorporated into an established GIS database of the NR colony, including daily positions of all seals (Twiss et al. [2000a](#), [2000b](#), [2001](#), [2003](#)). LOCs for individual mothers were calculated as above. Interannual associations between pairs of mothers were determined by generating lists of associated pairs of mothers within each year as above and comparing the lists of associations between years for repeat pairings.

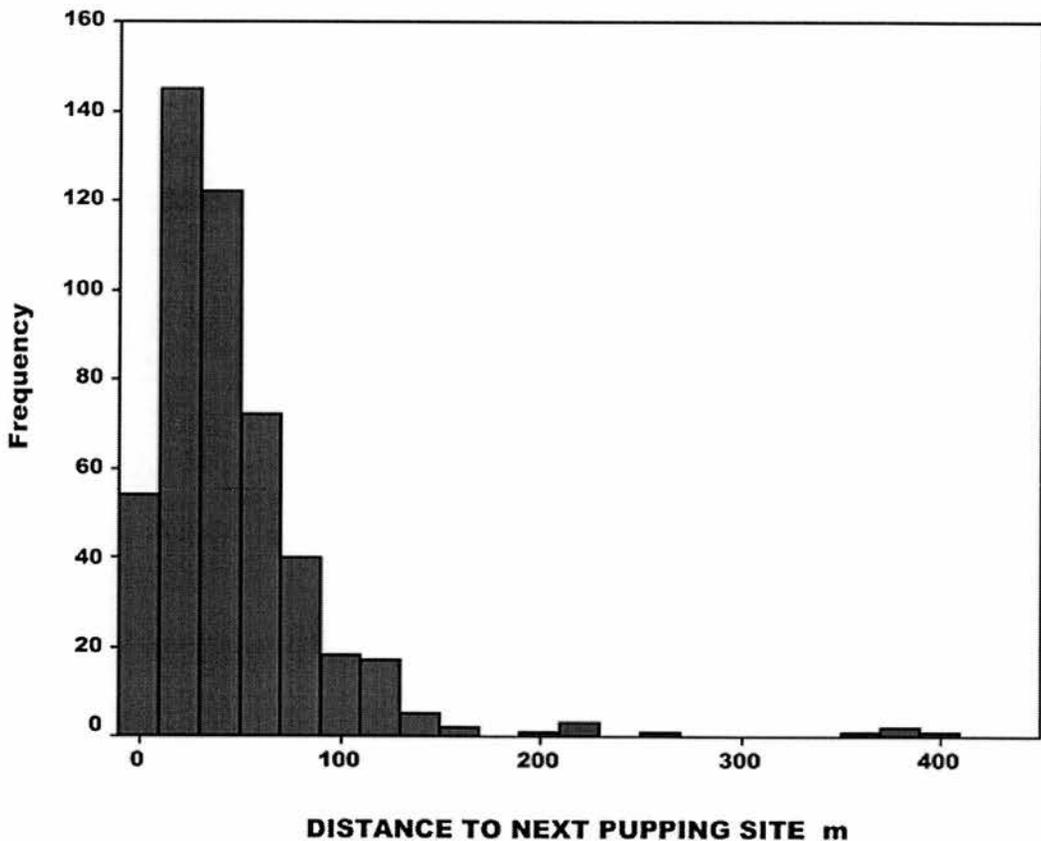
## Modelling the probability of association

A Monte Carlo approach was used to model the probability that a pair of mothers, recorded as associated in year 1, would be associated in year 2 within the norms of observed behaviour regarding pupping site fidelity and parturition date variability.

## Spatial association

The distance moved between pupping sites was assumed to conform to the distribution of observed site fidelity. The distance between pupping locations in consecutive years was measured for 484 cases from 182 known mothers that were present with a pup on NR between 1985 and

2001. These measures were used to produce a histogram of site fidelity distances (Fig. 2) from which a probability density function of pupping site movements was generated. Pupping locations within the NR colony can be separated by long distances (>800 m), but studies of branded animals (Pomeroy et al. 1994, 1999) involving surveys of alternative sites suggest that this is unusual. If births were not observed directly the pupping site of a known female was recorded as the mid-point of the 10 m×10 m grid cell in which she was first observed with a pup, subject to the pup's age at first sighting being 3 days or less. The bearing from north between successive pupping sites was measured to the nearest 5° for a subsample of 70 known mothers whose location was recorded in consecutive years. Data were pooled so that movements on bearings between (and including) 0°–45°, 45°–90°, 90°–135°, 135°–180°, 180°–225°, 225°–270°, 270°–315° and 315°–360° were grouped together. As there was no evidence of departure from a random direction of travel for these mothers ( $\chi^2=11.14$ ,  $df=7$ ,  $P>0.05$ ), it was assumed that a mother's pupping sites were located without bias of direction from one year to the next.



**Fig. 2** Observed pupping site fidelity distances for known mothers on North Rona between 1982 and 2000 ( $n=321$ )

Pupping site choice was assumed to be limited to those locations actually used by seals. A coverage comprising all locations of females mapped during the 2000 breeding season was used as the set of all potential locations within the SA to which mothers breeding in 1998 or 1999 could have moved. Locations outside the SA were not considered in the model as we found that only 3/478 (0.6%) of interannual movements went outside the limits of the SA.

Given an initial LOC for each female in year 1, the model redistributed mothers within potential pupping sites, weighting the likelihood of occupying any location by the site fidelity probability of the distance from the start point. Pairs of mothers from those located in 1998 or 1999 were defined as spatially associated according to the criteria above. Each mother was then relocated 5,000 times according to the procedure above and the distance separating any pair of relocated mothers (A, B) in year 2 was recalculated. The outcome of each replicate was scored as positive if mothers A and B were within 20 m of each other in year 2, and negative otherwise. No allowance was made in the model for the fact that females may not return every year, and even if they do, that they may not give birth. Only well-marked and recognisable animals were included, which may artificially increase the proportion of resightings. However, high resight rates were recorded for females identified by pelage markings during the study (80–100%, Redman *2002*), and these were comparable to those recorded for artificially marked animals (Pomeroy et al. *1994, 1999*).

## **Temporal association**

Known mothers in our 1999 sample pupped from 22 September to 23 October, pup date = 9 October  $\pm$  7.3 days (mean  $\pm$  SD). The distribution of pupping dates observed for these mothers was used to generate two lists of 5,000 pupping dates, pairs from which were classified according to our “within 9-day” criteria for association.

Mothers tend to pup on or around the same date in consecutive years, but with enough variation to make this important (day difference =  $-0.778 \pm 4.18$ , mean  $\pm$  SD,  $n=45$  mothers). The probability density function of change in pupping date was used to adjust the 5,000 pairs of simulated pupping dates and the list of 5,000 pairs was then retested for temporal association. Likelihood of temporal association was calculated as the proportion of original associates (3,205/5,000) which remained associated after simulated pupping date adjustment (2,417/3,205), giving a likelihood that existing temporal associations were retained between years of 0.75. Final expected association probabilities were calculated as the product of spatial and temporal probabilities.

---

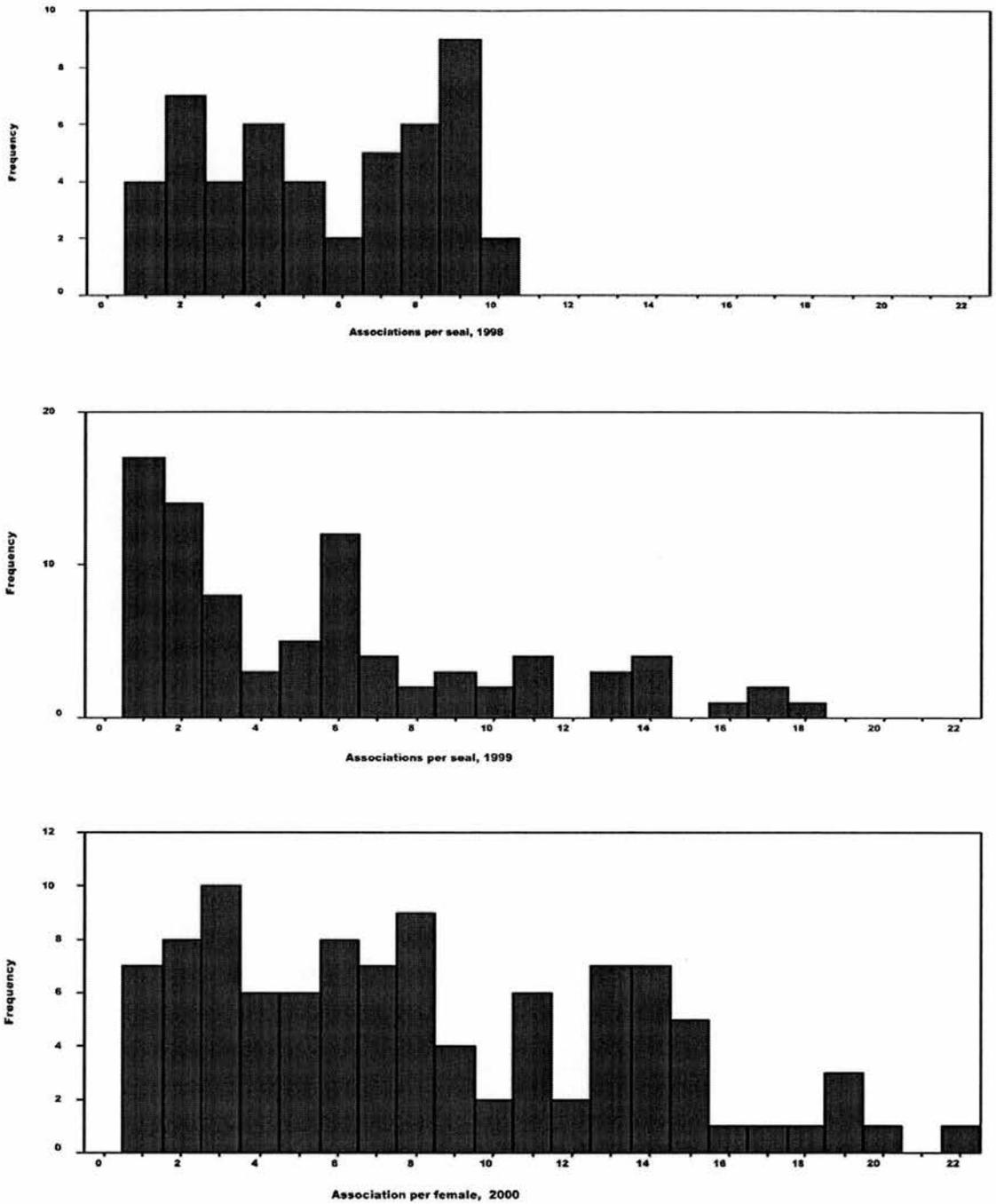
## Results

### Observed data: frequency of within-year associations

The locations of 60, 149 and 111 identifiable mothers were mapped from 1 to 22 days during their lactation periods in the seasons 1998, 1999 and 2000, respectively. Repeated daily locations and pupping dates (and therefore reliable association estimates) were available for 49, 90 and 94 mothers in each year respectively (Table 1). Within years, individual mothers had a maximum of 10 associates in 1998, 18 in 1999 and 22 in 2000 (Fig. 3).

**Table 1** Numbers of identified mothers used in study of associations and the number of associations between these on North Rona, 1998–2000. Total number of mothers identified during three seasons was 176; 160 of these were involved in measurable associations. We define a single pairwise association as being made up of two one-way associations

Year	1998	1999	2000
Number of mothers identified and located daily with known birth date (no. identified)	49 (60)	90 (149)	94 (111)
Number of pairwise associations (no. mothers involved)	135 (49)	309 (90)	274 (94)
Number of one-way associations in those above	270	618	548
One-way associations for mothers from 1998 (no. mothers involved)	270 (49)	131 (28)	162 (13)
One-way associations for mothers from 1999 (no. mothers involved)		487 (62)	175 (28)
One-way associations for mothers from 2000 (no. mothers involved)			211 (53)



**Fig. 3** The distribution of associations per female within the study area on North Rona in 1998 ( $n=49$ ), 1999 ( $n=90$ ) and 2000 ( $n=94$ )

### Observed data: frequency of between-year associations

The changes in associations between years can be best illustrated with examples from Tables 1 and 2. Although 49 mothers had 135 associations among themselves in 1998, only 28 of these mothers were available for consideration in 1999 (Table 1). These 28 mothers had 61 pairwise

associations among themselves in 1998. In 2000, the 41 mothers that were also present in 1999 had 65 pairwise associations with each other, 7 of which were repeated from the previous year (Table 2). Between 98/99 and 99/00 a total of 14 pairwise associations from 126 were the same in consecutive years. None were the same in all 3 years.

**Table 2** Number of repeated associations between years amongst identified mothers used in measures of associations on North Rona, 1998–2000

Years	1998–1999	1999–2000
Number of mothers in common	28	41
Total number of pairwise associations in year 1 within those mothers above	61	65
Pairwise year 1 associations repeated in year 2	7	7

### Observed data: joint distribution of site fidelity distances for mothers associated between years

The median distance between successive pupping sites of the known mothers in this study was 39 m ( $q_1=20$  m,  $q_3=68$  m,  $n=321$ , Fig. 2). Almost half of the pairs of mothers that were associated again in different years had each changed their pupping sites by more than the median site fidelity distance ( $6/14=43\%$ , Table 3).

**Table 3** Frequency table of distances moved between pupping sites by 14 pairs of known mothers that were spatially associated in 2 years on North Rona between 1998 and 2000

Distance moved (m)	Female A								
	0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80+
Female B	0–10	0							
	10–20	6	0						
	20–30	1	1 <sup>a</sup>	0					
	30–40	0	0	0	0				
	40–50	0	0	0	0	0			
	50–60	0	0	0	0	2	0		
	60–70	0	0	0	0	1	1	0	
	70–80	0	0	0	0	0	0	0	0
	80+	0	0	0	0	0	1	1	0

<sup>a</sup> The one case where one female moved 10–20 m and the other moved 20–30 m

## Model predictions: probability of interannual association

The paired pupping site displacement distance combinations for mothers A and B between years derived from 5,000 runs of the model followed the site fidelity distribution and indicated that shorter distance displacements were generally more likely than longer distance displacements. The probability that both mothers' pupping sites were displaced 10–20 m between years was more than six times greater than if both moved 70–80 m between years. In addition, the probability of an association between a pair of mothers being retained after they had moved the respective distances was largest for short distance moves, declining steadily as the distance between pupping sites increased. In the same examples highlighted as in Table 2, 46% of pairs that travelled 10–20 m were spatially associated in the second year and 19% of pairs that travelled 70–80 m were associated in the second year. The joint probability that the pupping sites of a pair of associated mothers were displaced by the distances shown and that the mothers remained spatially associated in the second year decreased rapidly with the distance separating mothers in a pair (Table 4). When the effects of temporal association had been included, even a pair of mothers whose pupping sites both changed by as little as 10–20 m had only a 0.01 chance of remaining associated in their second year (Table 4a). Mothers whose pupping sites were further apart had an even smaller probability of association in year 2.

**Table 4** Model output showing the joint probability that the pupping sites of associated mothers A and B would have been (1) displaced by the respective distances shown, (2) remain associated (within 20 m of one another) in year 2, and (3) remain temporally associated, according to the model's assumptions

Distance moved (m)	Female A									
	0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80+	
Female B	0–10	0.0075	0.0075	0.0036	0.0010	b	b	b	b	b
	10–20	0.0075	0.0087 <sup>a</sup>	0.0050	0.0023	0.0005	b	b	b	b
	20–30	0.0031	0.0046	0.0040	0.0030	0.0012	0.0003	b	b	b
	30–40	0.0007	0.0019	0.0027	0.0030	0.0018	0.0006	0.0001	b	b
	40–50	0.0001	0.0004	0.0009	0.0016	0.0016	0.0009	0.0004	0.0001	b
	50–60	b	b	0.0002	0.0005	0.0008	0.0007	0.0005	0.0003	b

Distance moved (m)	Female A								
	0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80+
60–70	b	b	b	0.0001	0.0003	0.0005	0.0006	0.0005	0.0001
70–80	b	b	b	b	b	0.0003	0.0004	0.0005 <sup>a</sup>	0.0003
80+	b	b	b	b	b	b	0.0001	0.0003	0.0010

<sup>a</sup> See text

<sup>b</sup>  $P < 0.0001$

### Comparison of observed association data and model predictions

Data for pupping site displacements were rearranged into cumulative distance classes to compare model predictions with observed data (Table 5). The expected probability of mother-pairs being associated in the second year, after both mothers returned to within 40 m of their previous pupping site, was 0.066, which is similar to the observed number of associated female-pairs that returned to within 40 m of their pupping site ( $8/126=0.063$ ). That is, these associated pairs could be explained by observed site fidelity, temporal fidelity and site preferences. However, there was a marked difference between the number of mothers that remained associated after larger displacements (>40 m) compared to the model's predictions. Mothers that were more than 40 m from their previous pupping site had a 0.010 chance of remaining associated according to the model, but the number of mother-pairs that remained associated after moving this distance was  $6/126=0.048$ , almost a factor of five greater (Table 5). This difference was significant ( $G_{adj}=15.7$ ,  $df=1$ ,  $P < 0.001$ ) indicating that maintenance of associations by mothers on NR after substantial changes in pupping sites cannot be explained by our model.

**Table 5** The model's expected probabilities of two associated mothers remaining associated after both moving the cumulative distances shown, compared with observed data for known mothers from North Rona 1998–2000

Pupping site displacement distances for each of mothers A and B	>0 m	>10 m	>20 m	>30 m	>40 m	>50 m	>60 m
	Modelled data						
Probability of both mothers moving distance shown and remain associated due	0.085	0.054	0.030	0.018	0.010	0.0061	0.0038

Pupping site displacement distances for each of mothers A and B	>0 m	>10 m	>20 m	>30 m	>40 m	>50 m	>60 m
to passive association							
Observed data							
Cumulative number of female-pairs that remained associated after travelling distance shown	14/126	7/126	6/126	6/126	6/126	3/126	1/126
Probability	0.111	0.056	0.048	0.048	0.048	0.024	0.008

## Discussion

Sociality forms a vital link between individuals and population structure (Michod 1999). Social groupings evolve when the benefits to participants produce selective advantages such as increased foraging efficiency, predator avoidance or reproductive advantages which outweigh any disadvantages that accrue (e.g. Trillmich 2002). However ecological factors are often responsible for aggregations of pinnipeds, ungulates, primates or birds because limiting resources such as areas suitable for foraging, drinking, resting or breeding are distributed patchily (Danchin and Wagner 1997). Studies of the evolution of animal aggregations and colonial living have generated many hypotheses, both ecological and social, to explain the emergence of sociality (Danchin and Wagner 1997; Sterck et al. 1997; Connor et al. 1999). These include economic benefits, predator avoidance and in particular, breeding habitat selection. Selectivity cannot only be based upon the habitat suitability of potential breeding sites, but also on conspecific attraction, including the presence of potential reproductive partners. Where mate attraction is important, it brings into focus the role of specific individuals, rather than “any” conspecific (such as may be the case in predator avoidance strategies) in determining the form of animal aggregations. However, relatively little attention has been paid to same-sex social relationships in non-cooperatively breeding mammals, with obvious exceptions being primate studies (Sterck et al. 1997) and male coalitions (e.g. Connor et al. 1999). Here we demonstrate the existence of such social association amongst female grey seals and discuss the potential role, relevance and benefits to individuals of same-sex sociality in a colonial, temporarily aggregating mammal.

## Association within years

Using natural markings to identify individuals has allowed a more comprehensive and “hands-off” approach to examining the social

structure of female grey seals on the breeding colony (Redman *2002*). Over 91% of identified grey seal mothers whose daily locations were recorded on more than two dates showed intra-annual association with at least one other female in this study. This probably underestimates the true prevalence of associates for our known mothers, as not all identified females in the SA were followed throughout their time ashore, the few cases of known females present without pups were omitted and not all mothers were identified. Additionally, there was no indication that recently identified animals had any fewer associations than previously identified seals (Table 1).

## **Interannual associations**

The frequency of interannual association observed amongst mothers that had changed their pupping locations by more than average was much greater than predicted by our model. This is the first quantitative evidence that active association occurs amongst female grey seals on NR, with specific mothers choosing to be near one another and supports previous anecdotal evidence (Pomeroy et al. *2000b*).

Our model of pupping site use aims for biological realism. Only occupied locations within the SA are used as potential pupping sites and interannual movements must be weighted by the known site fidelity behaviour of the seals. Seals that are highly site faithful are more likely to be associated in consecutive years. It is not possible to distinguish between the model's predictions and coordinated behaviour of pairs of seals over small (<40 m) displacements. However, when known temporal and spatial behavioural variability is constrained by areas actually used by seals, the expected probabilities of reassociation quickly become small.

## **Are associations likely to persist outside of the breeding season?**

Many mammals that exhibit sociality during breeding maintain some degree of social grouping outside the breeding season. Associations which persist from year to year on breeding colonies may be sustained throughout the year if seals remain together. Information on the social systems of pinnipeds outside of the breeding season is scarce (e.g. McConnell *1986*; Thompson et al. *1991, 1996*; McConnell and Fedak *1996*). Satellite tracking of animals has provided some indications of similar individual movement patterns but the reasons for these remain obscure (e.g. Fedak et al. *1998*; Robson et al. *1998*). Summer resights on NR suggest that at least a third of adult females breeding on NR also use the island as a summer haul-out, providing the potential for reinforcement of breeding season associations (Redman and Pomeroy, personal observation). Temporary haul-outs may reinforce social bonds, or there may be more protracted coordinated movements.

Irrespective of the mechanism by which associations form and are maintained, the associated movements seen here suggest that locations of consecutive pupping sites for seals within colonies are non-independent because seals behave non-independently. It follows that movements of seals between breeding colonies could be non-independent. Contrasting changes in pup production at adjacent colonies within a metapopulation structure have been documented, for example, the UK grey seal population (Duck 2003; Gaggiotti et al. 2002) and for Steller's sea lion *Eumatopias jubatus* (Raum-Suryan et al. 2002). Coordinated movement and possible associations of multiple animals in these cases deserve further attention, particularly as different forms of sociality have been shown to have demographic and fitness consequences for other mammals, e.g. white rhinos, Shrader and Owen-Smith (2002) and sciurids, Devillard et al. (2004).

## **Sociality as a selective advantage in pinnipeds**

Otariids might appear to be the better candidates within the pinnipeds to look for evidence of sociality, if only between mothers and pups, because of their extended nursing periods and need to find pups in crowded rookeries after long foraging trips at sea. In contrast, most phocid seals have short breeding periods and abrupt weaning of offspring, with short contact times between conspecifics. Nevertheless, age/sex classes may remain separated outside the breeding season (grey seals; Pomeroy, personal observation). It is more likely then that same sex/age class associations may be favoured in such cases. Repeated and strong site fidelity in long-lived animals may build up familiarity with neighbours, whether or not they are related. Familiarity may then lead to behavioural modifications between the individuals concerned, which ultimately produce some measurable fitness benefit, either in reduced costs to the mother or in increased performance in raising offspring. Likely possibilities include reduction of aggression between familiar associates, or preferential access to limited resources (e.g. Twiss et al. 2000a, 2000b). Pomeroy et al. (2001) provide evidence of local variation in measures of reproductive success within the NR colony in relation to relatedness and topography.

## **Identity and kinship**

Long-term associations between individuals in groups of free-ranging animals have been used as indirect evidence of the ability to recognize and remember identities in carnivores, primates and seabirds (Smuts et al. 1987; Black 1996; Waser 1996). However, site fidelity rather than kin or individual recognition could have explained some of these groupings (Insley 2000). The first direct evidence of this ability in pinnipeds has been northern fur seal *Callorhinus ursinus* mothers retaining memories of their offspring's vocalizations for at least 4 years (Insley 2000). Captive Californian sea lions *Zalophus californianus* showed some evidence of nepotism in that they were found to associate preferentially with kin and were more aggressive and less affiliative to non-kin (Hanggi and

Schusterman *1990*). While the sea lion study was of a long-term captive group, it showed that the development of affiliative behaviour followed kinships. Anecdotal implications of individual recognition in phocids have come from studies recording mate fidelity when mothers had changed location on the NR colony (Amos et al. *1995*). In such cases kinship is unlikely to be a prompt to individual recognition. While sisters and mother–daughter pairs may cooccur, it is not obvious how animals of different ages would become associated, as pups are thought to be forced into independence by the abrupt weaning process and yearlings are seen infrequently with other age classes (Pomeroy et al. *2000b*). It is more probable that associations form within cohorts as pups leave the breeding colony and learn to forage, so that the structure of the colony at the time of the cohort's birth and subsequent movements of individuals are likely to determine the likelihood of associations. Theoretical work has shown that non-random associations can evolve where a process of environmental feedback occurs (Pepper and Smuts *2002*). The environmental feedback process requires only that a cooperative trait affects the quality of the local environment and that individuals are more likely to leave low quality than high quality environments (Pepper and Smuts *2002*). A further consequence of the Pepper and Smuts' model was the appearance of genetic similarity in groups, but at lower levels than those derived through common ancestry.

## **Linking ecological, demographic and social factors**

The physical landscape affects the probability of non-random association and therefore the opportunity for social evolution. Grey seals breed in a wide range of habitats, and it is instructive to consider the potential interactions of environmental and biological factors on our expectations of sociality in grey seals elsewhere. Grey seals show little sign of breeding site fidelity at Sable Island, a large, fairly uniform sandbank on Canada's east coast (Boness and James *1979*). Access to breeding areas is unrestricted, breeding areas are, for the present at least, in excess and the population is increasing steadily. It is difficult to see how sociality might emerge in seals in such a situation. At NR, access is restricted, breeding areas vary in quality but are in excess and the local population is either stable or decreasing. The Isle of May on Scotland's east coast has an increasing population and breeding areas have already covered much of the available space. Site fidelity of Isle of May breeders is more extreme than that of NR seals, which was related to the scale of topographic variation (Pomeroy et al. *2000a*). No measures of sociality are available yet for the Isle of May grey seals, but the benefits that accrue from sociality might be expected to become important in the more competitive situation that a crowded colony represents. By implication, other colonially breeding species breeding in habitats that are similarly diverse at the appropriate scale might also be expected to show varied degrees of sociality.

Typically, behavioural and landscape ecological variables are usually measured on very different spatial scales, and this has hindered the development of a conceptual framework, which could link the two disciplines (Lima and Zollner *1996*). The grey seal breeding system is one in which individual behaviour, habitat selection and ecology operate on similar and measurable scales. As demonstrated here, the effects of breeding habitat preferences can be decoupled from individual associations, at least when animals change locations.

The associations we observe here highlight the potential for “simple sociality” within colonial species; preferences for specific other individuals that are not directly related to reproduction, foraging or defence, but perhaps accruing the simple benefit of reduced aggression amongst neighbours. The evolution of mechanisms that reduce conflict between individuals is a phenomenon with consequences that range across all biological scales. Such mechanisms are now viewed as the primary force behind the emergence of higher levels of organisation within biological systems, from genes to populations (Michod *1999*). Detailed studies of the extent of social association within species such as the grey seal, where social structures are relatively simple, and an assessment of the demographic and ecological conditions that promote these associations, will contribute to a deeper understanding of the evolution of sociality within animal systems and a more encompassing socio-ecological theory.

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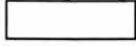
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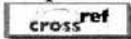
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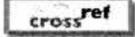
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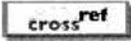
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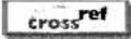


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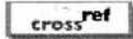
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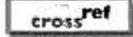
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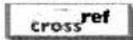


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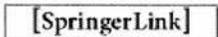
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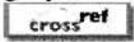
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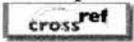
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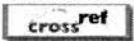


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# APPENDIX C

The raw input consists of four data files in .csv format containing the identities and locations of animals in year 1 (animalsfile), a list of all locations used in year 2 (possxyfile), the between year site fidelity probability distribution (pdffile), and list of association in year 1 (associationfile).

Data files:

animalsfile

id individual identifier (1,2,3,4...)  
x full OSGB x coordinate  
y full OSGB y coordinate

possxyfile

x full OSGB x coordinate  
y full OSGB y coordinate

pdffile

dist distance bin  
prob observed probability of moving within that distance bin

associationfile

A animal A of association pair  
B animal B of association pair

Function inputs:

C.1 "PR\_dist\_prob.fn"

animalsfile animalsfile  
possxyfile possxyfile  
pdffile pdffile

C.2 "PR\_sim.fn"

howmanyfiles number of "PR\_dist\_prob.fn" outputfiles  
iterations number of simulation iterations  
outputfile name of file to be created

C.3 "PR\_tabulate.fn"

simfile output file from "PR\_sim.fn"  
associationfile associationfile  
associationdistance distance over which social estimates are to be calculated  
newfiles names of file to be created

## APPENDIX C.1 "PR\_dist\_prob.fn" function for R

```

function (animalsfile,possxyfile,pdffile){

## read in data
animals<-read.table(animalsfile,header=T,sep=",")
possxy<-read.table(possxyfile,header=T,sep=",")
pdf<-read.table(pdffile,header=T,sep=",")

## create a file for each animal with distance to all possxy's
for(r in 1:nrow(animals)){
## create dist and prob vectors and add to temp file for all possxy's (and
rename)
names<-c("x","y","dist","prob")
dist<-rep(NA,nrow(possxy))
prob<-rep(NA,nrow(possxy))
temp<-data.frame(possxy$x,possxy$y,dist,prob)
names(temp)<-names
## calculate dist vector
temp$dist<-sqrt(abs(temp$x-animals$x[r])^2+abs(temp$y-animals$y[r])^2)
## calculate prob vector
temp$prob<-pdf$prob[temp$dist+1]

## change prob vector by dividing it by the availability of locations in 10m
radii bins
## create temp2 df
dist<-seq(0,499)
freq<-rep(0,500)
temp2<-data.frame(dist,freq)

## start loop over all possxys to make add up frequencies
for(i in 1:nrow(temp)){
temp2[temp[i,3]+1,2]<-temp2[temp[i,3]+1,2]+1
}

## bin into 10m bins
temp2[1:10,2]<-sum(temp2[1:10,2])
temp2[11:20,2]<-sum(temp2[11:20,2])
temp2[21:30,2]<-sum(temp2[21:30,2])
temp2[31:40,2]<-sum(temp2[31:40,2])
temp2[41:50,2]<-sum(temp2[41:50,2])
temp2[51:60,2]<-sum(temp2[51:60,2])
temp2[61:70,2]<-sum(temp2[61:70,2])
temp2[71:80,2]<-sum(temp2[71:80,2])
temp2[81:90,2]<-sum(temp2[81:90,2])
temp2[91:100,2]<-sum(temp2[91:100,2])
temp2[101:110,2]<-sum(temp2[101:110,2])
temp2[111:120,2]<-sum(temp2[111:120,2])
temp2[121:130,2]<-sum(temp2[121:130,2])
temp2[131:140,2]<-sum(temp2[131:140,2])
temp2[141:150,2]<-sum(temp2[141:150,2])
temp2[151:160,2]<-sum(temp2[151:160,2])
temp2[161:170,2]<-sum(temp2[161:170,2])
temp2[171:180,2]<-sum(temp2[171:180,2])
temp2[181:190,2]<-sum(temp2[181:190,2])
temp2[191:200,2]<-sum(temp2[191:200,2])
temp2[201:210,2]<-sum(temp2[201:210,2])
temp2[211:220,2]<-sum(temp2[211:220,2])
temp2[221:230,2]<-sum(temp2[221:230,2])
temp2[231:240,2]<-sum(temp2[231:240,2])
.
.
.
.
temp2[491:500,2]<-sum(temp2[491:500,2])

temp$prob<-temp$prob/temp2$freq[temp$dist+1]

## save temp to file
filename<-paste("PR_",animals[r,1],"_possxy_dist_over_avail_prob.csv",sep="")
write.table(temp,file=filename,row.names=F,sep=",")
rm(temp)
}
}

```

APPENDIX C.2 "PR\_sim.fn" function for R

```
function (howmanyfiles, iterations, outputfile)
{
  ## create output file
  output<-data.frame(matrix(NA,nrow=iterations,ncol=howmanyfiles*3))
  ## create names vector
  names<-numeric(0)
  for(p in 1:howmanyfiles){names<-
  c(names,paste(p,"x",sep=""),paste(p,"y",sep=""),paste(p,"dist",sep=""))}
  names(output)<-names
  #print(output)

  #####
  for(i in 1:howmanyfiles){ # start loop over data files for each animal
  #####

  ## read in data
  filename<-paste("PR_",i,"_possx_y_dist_over_avail_prob.csv",sep="")
  temp<-read.table(filename,header=T,sep=",")
  #print(filename)
  #print(temp)

  ## add new xy and dist to output file for each iteration
  if(i==1){output[,1:3]<-
  temp[sample(nrow(temp), iterations, prob=temp$prob, replace=T), 1:3]}
  if(i>1){output[,(((i-1)*3)+1):(((i-1)*3)+3)]<-
  temp[sample(nrow(temp), iterations, prob=temp$prob, replace=T), 1:3]}

  ###
  } # end loop over data files
  ###

  ## save output
  write.table(output, file=outputfile, row.names=F, sep=", ")

  print(output)
}
```

## APPENDIX C.3 "PR tabulate.fn" function for R

```

function (simfile,associationfile,associationdistance,newfiles){

## read in data
simdata<-read.table(simfile,header=T,sep=",")
assoc<-read.table(associationfile,header=T,sep=",")
#print(simdata)
#print(assoc)

## create a file for animals that maintain assoc (adata) and those that don't
(nadata)
adata<-matrix(0,nrow=9,ncol=9)
nadata<-matrix(0,nrow=9,ncol=9)
#print(adata)
#print(nadata)

## create index file to reference positions into adata and nadata (ie. bin 0-
10=1, 10-20=2 ...80+ =9)
index<-c(rep(1:8,each=10),rep(9,1000))
#index<-c(1,2,3,4,5,6,7,8,9,10)

j<-nrow(assoc) #
for(i in 1:j){ # start loop over associated animals from '99

print(paste("pair",i))

## for each pair calculate the distance between them in iterations in a one'er
dist<-sqrt(abs(simdata[,((assoc$A[i]-1)*3)+1])-simdata[,((assoc$B[i]-
1)*3)+1])^2+abs(simdata[,((assoc$A[i]-1)*3)+2])-simdata[,((assoc$B[i]-
1)*3)+2])^2)
#print(dist)

q<-nrow(simdata) #
for(p in 1:q){ # start loop over iterations in simfile

ifelse(dist[p]<=associationdistance,
adata[index[(simdata[p,((assoc$B[i]-
1)*3)+3])+1],index[(simdata[p,((assoc$A[i]-1)*3)+3])+1]]<-
adata[index[(simdata[p,((assoc$B[i]-
1)*3)+3])+1],index[(simdata[p,((assoc$A[i]-1)*3)+3])+1]]+1
,
nadata[index[(simdata[p,((assoc$B[i]-
1)*3)+3])+1],index[(simdata[p,((assoc$A[i]-1)*3)+3])+1]]<-
nadata[index[(simdata[p,((assoc$B[i]-
1)*3)+3])+1],index[(simdata[p,((assoc$A[i]-1)*3)+3])+1]]+1
)
) # end loop over iterations

} # end loop over associated animals from'99

## create probability matrix
names<-c("0-10","10-20","20-30","30-40","40-50","50-60","60-70","70-80","80+")
#names<-c("1","2","3","4","5","6","7","8","9")

adata<-data.frame(adata,row.names=names)
names(adata)<-names
print("count of pairs that stayed in association given certain movements")
print(adata)
filename<-paste(newfiles,"_adata.csv",sep="")
write.table(adata,file=filename,sep=" ",row.names=F)

nadata<-data.frame(nadata,row.names=names)
names(nadata)<-names
print("count of pairs that did not stay in association given certain movements")
print(nadata)
filename<-paste(newfiles,"_nadata.csv",sep="")
write.table(nadata,file=filename,sep=" ",row.names=F)

}

```

# APPENDIX D

D.1 "RR dist over avail\_prob.fn"

input: (input02,possxy,sitefid)

this produces a file for each resident mother with the probability of moving to each of the possible locations in possxy

input02 eg: "FINAL\_BY\_centroids02\_20m.csv"

file with columns: name, id0203, x, y, pupdate

centroid locations of resident mothers

possxy eg: "possxy\_2daypuplocs\_centroids03inmyarea.csv"

file with columns: location, x, y

this file was created by joining all stage 1 pup locations at two day intervals outwith my area in 2003 with centroid locations within my area from 2003.

sitefid eg: "sitefid\_0203.csv"

file with columns: sitefid, prob

probability distribution of site fidelity movements from 2002 to 2003

D.1 " RR\_sim.fn"

input: (data02,possxyfile,iterations,outputfile)

data02:

as above

possxyfile:

as above

iterations:

the number of simulations to be carried out eg: 5000

outputfile:

prefix to each file created during the sim

## APPENDIX D.1 "RR dist over avail prob.fn" function for R

```

function (input02,possxy,sitefid)
{
data<-read.csv(input02)
possxy<-read.csv(possxy)
sitefid<-read.csv(sitefid)

# create a file for each animal
for(i in 1:nrow(data)){
  names<-c("location","x","y","dist","prob")
  dist<-rep(NA,nrow(possxy))
  prob<-rep(NA,nrow(possxy))
  animfile<-data.frame(possxy$location,possxy$x,possxy$y,dist,prob)
  names(animfile)<-names

  animfile$dist<-sqrt((data$x[i]-animfile$x)^2+(data$y[i]-animfile$y)^2)
  animfile$prob<-sitefid$prob[animfile$dist+1]
  if(i==2)print(animfile)

  # count number of distances in 10m bins
  d<-rep(0,450)
  for(l in 1:nrow(animfile)){d[animfile$dist[l]+1]<-d[animfile$dist[l]+1]+1}
  if(i==2)print(d)
  d[1:10]<-sum(d[1:10])
  d[11:20]<-sum(d[11:20])
  d[21:30]<-sum(d[21:30])
  d[31:40]<-sum(d[31:40])
  d[41:50]<-sum(d[41:50])
  d[51:60]<-sum(d[51:60])
  d[61:70]<-sum(d[61:70])
  d[71:80]<-sum(d[71:80])
  d[81:90]<-sum(d[81:90])
  d[91:100]<-sum(d[91:100])
  d[101:110]<-sum(d[101:110])
  d[111:120]<-sum(d[111:120])
  d[121:130]<-sum(d[121:130])
  d[131:140]<-sum(d[131:140])
  d[141:150]<-sum(d[141:150])
  d[151:160]<-sum(d[151:160])
  d[161:170]<-sum(d[161:170])
  d[171:180]<-sum(d[171:180])
  d[181:190]<-sum(d[181:190])
  d[191:200]<-sum(d[191:200])
  d[201:210]<-sum(d[201:210])
  d[211:220]<-sum(d[211:220])
  d[221:230]<-sum(d[221:230])
  d[231:240]<-sum(d[231:240])
  d[241:250]<-sum(d[241:250])
  d[251:260]<-sum(d[251:260])
  d[261:270]<-sum(d[261:270])
  d[271:280]<-sum(d[271:280])
  d[281:290]<-sum(d[281:290])
  d[291:300]<-sum(d[291:300])
}}

.
.
.
.
d[411:420]<-sum(d[411:420])
d[421:430]<-sum(d[421:430])
d[431:440]<-sum(d[431:440])
d[441:450]<-sum(d[441:450])

if(i==2)print(d)
# Divide probabilities by count of locations in respective 10m bin
for (l in 1:nrow(animfile)){
  animfile$prob[l]<-animfile$prob[l]/d[animfile$dist[l]+1]
}

if(i==2)print(animfile)

filename<-paste("BY_",data[i,2],"_possxy_sitefid_over_avail_prob.csv",sep="")
write.table(animfile,file=filename,sep=" ",row.names=F)
}}

```

## APPENDIX D.1 "RR\_sim.fn" function for R

```

function (data02,possxyfile,iterations,outputfile)
{

data02<-read.csv(data02)
returnrate<-numeric(0)

for(sim in 1:iterations){
possxy<-read.csv(possxyfile)
output<-as.data.frame(matrix(NA,nrow=nrow(data02),ncol=6))
names(output)<-c("name","id0203","location","x","y","pupdate")

## for each animal in data02, redistribute due to site fidelity

  for(i in data02$id0203[1:nrow(data02)]){
    # read in data
    filename<-paste("BY_",i,"_possxy_sitefid_over_avail_prob.csv",sep="")
    temp<-read.csv(filename)
#print(temp)
    # delete locations already taken from temp
    if(i>1){
      a<-output$location[1:i-1]
      #print(a)
      # delete these locations from temp
      for(loc in 1:length(a)){temp<-temp[-
which(temp$location==a[loc]),]}
#print(temp)
      # pick a new xy
      output[which(data02$id0203==i),3:5]<-
temp[sample(nrow(temp),1,prob=temp$prob),1:3]

      # add name/number/pupdate
      output[which(data02$id0203==i),1]<-
as.character(data02[which(data02$id0203==i),1])
      output[which(data02$id0203==i),c(2,6)]<-
data02[which(data02$id0203==i),c(2,5)]

#print(output[1:5,])

    } # end loop over animals

output<-output[,-3]
#filename<-paste(outputfile,sim,".csv",sep="")
#print(filename)
#write.table(output,file=filename,sep=" ",row.names=F)

### Calculate return rate between 2002 and this sim

  ## delete animals if outwith area observed in 2003
#   if(length(which(output$x<181290&output$x>=181370))!=0){
#     output<-output[-which(output$x<181290|output$x>=181370),]#}
#   if(length(which(output$y<1032620&output$y>=1032720))!=0){
#     output<-output[-which(output$y<1032620|output$y>=1032720),]#}
#   if(length(which(output$x>=181360&output$y>=1032710))!=0){
#     output<-output[-which(output$x>=181360&&output$y>=1032710),]}
#   if(length(which(output$x<181300&output$y>=1032700))!=0){
#     output<-output[-which(output$x<181300&output$y>=1032700),]}
#   if(length(which(output$x<181310&output$y>=1032710))!=0){
#     output<-output[-which(output$x<181310&output$y>=1032710),]}

returnrate[sim]<-nrow(output)/nrow(data02)

} # end loop over sims

#print(output[1:5,])
print(returnrate)
print(paste("mean return rate:",mean(returnrate)))
print(quantile(returnrate,probs=c(0.025,0.975)))
# save returnrate output
write.table(returnrate,file=outputfile,sep=" ",row.names=F,col.names=F)
}

```

# APPENDIX E

E.1 "dist over avail\_prob.fn"

input: (input02,possxy,sitefid)

this produces a file for each neighbour of the focal animal with the probability of moving to each of the possible locations in possxy

input02 eg: "assocs\_20m9d\_ax02.csv"

file with columns: name, id0203, x, y, pupdate

the first entry should be the focal animal

subsequent entries are those associates in 2002 (eg. within20m and 9d)

possxy eg: "possxy\_2daypuplocs\_centroids03inmyarea\_Ax.csv"

file with columns: location, x, y

this file was created by joining all stage 1 pup locations at two day intervals

outwith my area in 2003 with centroid locations within my area from 2003.

the location of the focal animal is removed so that it can not be taken by another.

sitefid eg: "sitefid\_0203.csv"

file with columns: sitefid, prob

probability distribution of site fidelity movements from 2002 to 2003

E.2 "sim.fn"

input: (data02,data03,possxyfile,tempfid,iterations,outputfile,pupdates)

this produces a file for each simulation. the focal animal's location and birth date are as observed in 2003. each of it's associates from 2002 are moved to a possxy location due to site fidelity probabilities as calculated above and have pup date changed due to temporal fidelity distribution. All remaining possxys are populated with new animals with pupdates taken from the observed distribution of pup dates in 2003. SS is then calculated at 20m radius and 9 day time window around focal animal from 2002 to each sim.

data02 eg: "assocs\_20m9d\_ax02.csv"

data03 eg: "FINAL\_BY\_centroids03\_20m.csv"

this is the observed centroid locations and pupdates for animals in 2003

possxyfile eg: "possxy\_2daypuplocs\_centroids03inmyarea\_Ax.csv"

tempfid eg: "tempfid\_0203.csv"

file with columns: tempfid, prob

probability distribution of temporal fidelity of pup dates from 2002 to 2003

iterations: the number of simulations to be carried out eg: 5000

outputfile: eg: "BY\_ax\_sim1to5000\_"

prefix to each file created during the sim

pupdates eg: "pupdates\_0203.csv"

file with columns: bd03, prob. probability distribution of pup dates from 2003

## APPENDIX E.1 "dist over avail prob.fn" function for R

```

function (input02,possxy,sitefid)
{

data<-read.csv(input02)
possxy<-read.csv(possxy)
sitefid<-read.csv(sitefid)

# create a file for each neighbour
for(i in 2:nrow(data)){
  names<-c("location","x","y","dist","prob")
  dist<-rep(NA,nrow(possxy))
  prob<-rep(NA,nrow(possxy))
  animfile<-data.frame(possxy$location,possxy$x,possxy$y,dist,prob)
  names(animfile)<-names

  animfile$dist<-sqrt((data$x[i]-animfile$x)^2+(data$y[i]-animfile$y)^2)
  animfile$prob<-sitefid$prob[animfile$dist+1]
if(i==2)print(animfile)

  # count number of distances in 10m bins
  d<-rep(0,450)
  for(l in 1:nrow(animfile)){d[animfile$dist[l]+1]<-d[animfile$dist[l]+1]+1}
if(i==2)print(d)
  d[1:10]<-sum(d[1:10])
  d[11:20]<-sum(d[11:20])
  d[21:30]<-sum(d[21:30])
  d[31:40]<-sum(d[31:40])
  d[41:50]<-sum(d[41:50])
  d[51:60]<-sum(d[51:60])
  d[61:70]<-sum(d[61:70])
  d[71:80]<-sum(d[71:80])
  d[81:90]<-sum(d[81:90])
  d[91:100]<-sum(d[91:100])
  d[101:110]<-sum(d[101:110])
  d[111:120]<-sum(d[111:120])
  d[121:130]<-sum(d[121:130])
  d[131:140]<-sum(d[131:140])
  d[141:150]<-sum(d[141:150])
  d[151:160]<-sum(d[151:160])
  d[161:170]<-sum(d[161:170])
  d[171:180]<-sum(d[171:180])
  d[181:190]<-sum(d[181:190])
  d[191:200]<-sum(d[191:200])
  d[201:210]<-sum(d[201:210])
  d[211:220]<-sum(d[211:220])
  d[221:230]<-sum(d[221:230])
  d[231:240]<-sum(d[231:240])
  d[241:250]<-sum(d[241:250])
  d[251:260]<-sum(d[251:260])
  d[261:270]<-sum(d[261:270])
  d[271:280]<-sum(d[271:280])
  d[281:290]<-sum(d[281:290])
  .
  .
  .
  d[411:420]<-sum(d[411:420])
  d[421:430]<-sum(d[421:430])
  d[431:440]<-sum(d[431:440])
  d[441:450]<-sum(d[441:450])

if(i==2)print(d)
  # Divide probabilities by count of locations in respective 10m bin
  for (l in 1:nrow(animfile)){
    animfile$prob[l]<-animfile$prob[l]/d[animfile$dist[l]+1]
  }

if(i==2)print(animfile)

  filename<-
paste("BY_",data[i,2],"_possxy_sitefid_over_avail_prob.csv",sep="")
  write.table(animfile,file=filename,sep=" ",row.names=F)
}}

```

## APPENDIX E.2 "sim.fn" function for R

```

function (data02,data03,possxyfile,tempfid,iterations,outputfile,pupdates)
{

data02<-read.csv(data02)
data03<-read.csv(data03)
tempfid<-read.csv(tempfid)
pupdates<-read.csv(pupdates)
SS<-numeric(0)

for(sim in 1:iterations){
possxy<-read.csv(possxyfile)
output<-as.data.frame(matrix(NA,nrow=nrow(possxy)+1,ncol=6))
names(output)<-c("name","id0203","location","x","y","pupdate")

## retain movement / pupdate of focal animal as observed
focalanimal<-data02$id0203[1]
output$name[1]<-as.character(data03$name[which(data03$id0203==focalanimal)])
output$id0203[1]<-focalanimal
output[1,4:6]<-data03[which(data03$id0203==focalanimal),3:5]
#print(output[1,])

## for each neighbour in data02, redistribute due to site and temp fidelity

  for(i in data02$id0203[2:nrow(data02)]){
    # read in data
    filename<-
paste("BY_",i,"_possxy_sitefid_over_avail_prob.csv",sep="")
    temp<-read.csv(filename)
#print(temp)
    # delete locations already taken from temp
    if(which(data02$id0203==i)>2){
      m<-which(data02$id0203==i)-1
      a<-output$location[2:m]
      #print(a)
      # delete these locations from temp
      for(loc in 1:length(a)){temp<-temp[-
which(temp$location==a[loc]),]}
#print(temp)
      # pick a new xy
      output[which(data02$id0203==i),3:5]<-
temp[sample(nrow(temp),1,prob=temp$prob),1:3]

      # add name/number/pupdate
      output[which(data02$id0203==i),1]<-
as.character(data02[which(data02$id0203==i),1])
      output[which(data02$id0203==i),c(2,6)]<-
data02[which(data02$id0203==i),c(2,5)]

      # change pupdate by tempfid!
      output[which(data02$id0203==i),6]<-
output[which(data02$id0203==i),6]+sample(tempfid$tempfid,1,prob=tempfid$prob)
#print(output[1:5,])

    } # end loop over neighbours

  # populate remainder of output with remainder of locations from possxy,
new ids and pupdates
  a<-output$location[2:nrow(data02)]
  for(loc in 1:length(a)){possxy<-possxy[-
which(possxy$location==a[loc]),]}
  output[(nrow(data02)+1):nrow(output),3:5]<-possxy
  output[(nrow(data02)+1):nrow(output),2]<-
seq(1000,by=1,length=nrow(output)-nrow(data02))
  output[(nrow(data02)+1):nrow(output),6]<-
sample(pupdates$dbd03,size=length((nrow(data02)+1):nrow(output)),prob=pupdates$pro
b,replace=T)

output<-output[,-3]
filename<-paste(outputfile,sim,".csv",sep="")
print(filename)
write.table(output,file=filename,sep=" ",row.names=F)

```

## APPENDIX E

---

```
## Calculate SS for focal animal between 2002 and this sim
assoc02<-data02$id0203[2:nrow(data02)]

## who are assocS in this sim?
output$dism<-sqrt((output$x-rep(output$x[1],nrow(output)))^2 + (output$y-
rep(output$y[1],nrow(output)))^2)
output$dismd<-output$pupdate-rep(output$pupdate[1],nrow(output))
output<-output[-which(output$dism>20|abs(output$dismd)>9),]
output<-output[-1,]
assocSIM<-output$id0203

## list all assocS
assoc02SIM<-c(assoc02,assocSIM)
index<-order(assoc02SIM)
assoc02SIM<-assoc02SIM[index]
#print(assoc02SIM)

## how many of these are the same from 02 to SIM
same<-numeric(0)
numbers<-length(assoc02SIM)
if(numbers>=2){
  for(number in 1:numbers){
    ifelse(
      ((assoc02SIM[number]+assoc02SIM[number+1])/2)==assoc02SIM[number],
      same<-c(same,assoc02SIM[number])
      ,NA)
  }
#print(paste("same:",same))
}
a<-length(same)
b<-length(assoc02)-length(same)
c<-length(assocSIM)-length(same)
#print(paste("a:",a))
#print(paste("b:",b))
#print(paste("c:",c))
SS<-c(SS,a/(a+b+c))

} # end loop over sims
#print(output[1:5,])
print(SS)
# save SS output
filename2<-paste(outputfile,"SS.csv",sep="")
write.table(SS,file=filename2,sep=" ",row.names=F,col.names=F)
}
```