DISPERSAL AND DISPERSION OF SOUTHERN ELEPHANT SEALS AT MARION ISLAND

by

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ABSTRACT

This study focused on the dispersal and dispersion of southern elephant seals, *Mirounga leonina*, at Marion Island in relation to their natal site, and to their site of first reproduction. Movements from the natal site to terrestrial haulouts used for reproduction, and between successive reproductive sites, were defined as dispersal, while movements from the natal site to sites used for purposes other than reproduction, were defined as dispersion. Some 33 000 records collected over 12 years, of haulouts at 54 different sites of 5700 tagged seals, formed the database analysed. Both male and female seals were found to use sites closer to their natal site than expected, for reproductive, moult and winter haulouts. However, breeding seals used sites closer to their site of first reproduction than their natal site, on subsequent reproductive haulouts. No difference was found between the mean distances dispersed to moult sites and to winter haulout sites, but distances of dispersal were significantly less than distances of dispersion. Female seals dispersed further than males to reproductive sites, but no difference between the sexes was apparent for moult and winter dispersion. While the number of male seals hauling out to reproduce was too small to assess the effects of various factors on the dispersal of males, a number of factors influenced the dispersion of male seals, and dispersion and dispersal of female seals. These included age, isolation of natal site, anthropogenic disturbance, natal harem size and natal harem pre-weaning mortality. A number of hypotheses are proposed to explain the reasons behind the results found, and the direction of future research concerning the movements of southern elephant seals and their choice of terrestrial environment is suggested.

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FOREWORD

This study concerns the movements of southern elephant seals from the population at Marion Island, and specifically, movements between the sites or beaches used by seals for the terrestrial phase of their life, and the distances that separate these sites. It therefore considers the dispersal and dispersion of elephant seals. These two terms, and a number of others, are defined in the first section of the introduction (Chapter 1). All definitions employed throughout this thesis are repeated in the glossary (Appendix one). The introduction also gives a background to dispersal and dispersion, a description of the study animal, a review of dispersal and dispersion in pinnipeds and a number of null hypotheses, the validity of which, this study attempts to assess. Chapter 2 covers the study site, briefly describing its location, topography and climate. Chapter 3 details the methods used, including fieldwork, manipulation of the database, statistical analyses and the assumptions. Further methods relevant to each section are given at the beginning of chapters 4 – 7. Each of these chapters, besides including a short methods section, describes results and discusses them. These discussions not only compare the results to those of other studies, but also propose hypotheses to account for the findings of this study. Chapter 4 establishes that elephant seals are philopatric, Chapter 5 considers the differences between various types of dispersal and dispersion, Chapter 6 notes differences between the sexes, and Chapter 7 deals with the influence of six different factors on the dispersal and dispersion of elephant seals. The final chapter (Chapter 8) attempts to draw all the findings together in a conclusive whole. It also posits a speculative synthesis, which is a description of elephant seal life history behaviour, of the population at Marion Island, in relation to terrestrial haulout sites. The study is accompanied by 7 appendices, which describe the pattern of possible elephant seal lifetime haulouts and give examples of lifetime haulout histories, describe aspects of the island and give details of a probability matrix used for the calculation of expected values. The study is condensed in the Abstract at the beginning, and a summary at the end.

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CHAPTER 1

INTRODUCTION

1.1 DISPERSAL AND DISPERSION

1.1.1 Definitions

Long-term movements of animals, that is, seasonal movements important on a life-history scale, can be defined in a number of ways. The vast body of literature that exists concerning these movements uses a variety of terms to define them (Reviewed in Baker 1978, Shields 1987). It is therefore necessary to define a number of terms at the outset. The definitions that follow, and others detailed later in this thesis, are repeated in Appendix 1. This should enable those confused by a barrage of terms to navigate their way through this thesis by quick reference to a glossary when the need arises.

The use of the term **dispersal** in this study follows the most widely used zoological definition. It is defined as the movement of an animal from its site of birth to a site, or sites where reproduction (mating or parturition) is attempted, irrespective of its success, and further movement between these sites. Inherent in this definition are two types of dispersal. The first is **natal dispersal**, which is the movement of an animal from its natal site to the site of first attempted reproduction. The second is **breeding dispersal**, which is movement from the site at which reproduction was first attempted to subsequent sites of attempted reproduction (partially after Howard 1960, Greenwood 1980, and Shields 1987). In this study, the distance an animal disperses refers specifically to the distance of the shortest practicable route it is able to take between two sites, and not necessarily to the distance of the path that it follows between those two sites.

Although the term **dispersion** often refers to distribution of individuals within space (Shields 1987) it has also been used to refer to the movements of individual animals for non-reproductive purposes (Nicholls 1970, Lenglart & Bester 1982, Riedman 1990, Wilkinson & Bester 1990, Lewis *et al.* 1996). The term dispersion is defined by exclusion, as the long-term movements of individual animals to sites where reproduction is not attempted.

Dispersion can include **migration**, defined here as regular seasonal movements between home ranges (Caughley 1977), but not **emigration** or **immigration**, which are movements of individuals out of, or into defined breeding groups or areas, and are forms of dispersal (Shields 1987).

Another term is **philopatry** (from the Greek, meaning, "love of home"), which is a return to reproduce at the natal site (Shields 1987). Associated with this term is **site fidelity**, which is defined as return to any site used in the past, including the natal site.

1.1.2 The importance of dispersal

The consequences of dispersal are important in considering population dynamics, population genetics and species survival.

Dispersal is one of three mechanisms by which population change is effected, the others being birth and death. Dispersal, however, concerns not only the number of individuals moving into and out of a population group. The age, reproductive status and sex of dispersing individuals, and the conditions under which they disperse, affect natality and mortality. Further, dispersing individuals usually experience greater mortality than do philopatric ones (Caughley 1977, Gaines & McClenaghan 1980, Moore & Ali 1984).

The genetic structure of a population can be defined in terms of the frequencies of various alleles in that population, and therefore the probabilities that an individual will carry particular alleles. The frequencies of alleles usually differ between populations due to a number of contingent and stochastic reasons. When animals transfer into or out of a population they change the allele frequency of that population. The number of individuals moving from one population to another has a considerable effect on the genetic composition of both populations (Caughley 1977, Gaines & McClenaghan 1980, Lidicker & Caldwell 1982).

One of the principle causes of the global decline in biodiversity is the fragmentation and destruction of natural populations (Diamond 1989). Large populations are split into smaller ones, and small populations become increasingly isolated. This makes dispersal between populations more difficult (Hanski & Gilpin 1991). Theoretically, adequate dispersal increases the probability of long-term population survival in a number of ways. (1) New genetic material is introduced, increasing the heterogeneity of a population and therefore, its ability to deal with change (Caughley 1977). (2) New genetic material also reduces the incidence of inbreeding depression (Packer 1979, Pusey 1980). (3) Suitable uninhabited areas are colonised allowing new populations to arise. These may replace extinct populations, and thereby increase the probability of maintaining a number of populations (Hanski & Gilpin 1991, Hanson 1991). (4) Dispersers are able to rescue populations with critically low numbers (Hanski & Gilpin 1991, Hanson 1991).

1.1.3 Why disperse?

Potentially, many benefits accrue to the individual through natal site fidelity. These include (1) maintaining a moderate level of inbreeding, which allows the maintenance of both locally adapted gene complexes and intrinsically co-adapted gene complexes (Bateson 1982, Shields 1987, Pusey & Wolf 1996), (2) adaptation to local conditions, (3) familiarity with the natal area and social group, (4) greater assurance of mates and other resources being available, and (5) cooperation with kin, which gives both direct benefits (e.g. it ameliorates aggression during competitive interactions and enables a territory to be maintained despite strong competition) and increases inclusive fitness (Shields 1987).

In addition to the benefits of site fidelity, many potential costs are inherent in dispersal. These include (1) outbreeding depression, (2) increased expenditure of time and energy on movement at the cost of reproductive and maintenance activities, (3) greater exposure to predation, parasitism and disease, (4) increased exposure to extreme weather conditions, (5) unfamiliarity with the local environment and lack of access to refuges, (6) higher levels of aggression from conspecifics, and (7) increased uncertainty of finding mates and other resources (Lidicker & Caldwell 1982, Waser & Jones 1983, Moore & Ali 1984, Shields 1987).

Given that there is a strong incentive for philopatry, and adequate reasons not to disperse, many animals still leave their natal site or population. Why? A number of reasons have been postulated to explain dispersal. The four most important are (1) reduced access to resources, (2) reduced access to mates, (3) increased competition with kin, and (4) avoidance of inbreeding (Caughley 1977, Lidicker & Caldwell 1982, Dobson & Jones

1985). Other reasons proposed include habitat changes (Caughley 1977, Cooch *et al.* 1993, Aebischer 1995) and the need to leave refuges infested with excessive numbers of parasites (Brown & Brown 1992).

Attempts to explain dispersal often involve looking at patterns of sex and age bias characteristic of birds and mammals. Typically, dispersers are immatures. Males are the predominantly dispersing sex in most species of mammals, whereas females are in most species of birds (Greenwood 1980, Dobson 1982). These patterns have been explained by reference to a species' social structure and its social adaptation to the environment. Greenwood (1980) suggested that the mating system determined which sex would tend to disperse. In systems where males defended resources to which females were attracted, dispersal would be female biased. Males would have the most to gain from philopatry since familiarity with an area would favour their chances of obtaining and keeping a territory. In addition, groups of related males would be able to support one another in maintaining a territory. In systems where males defended access to mates and associated reproductive opportunities, dispersal would be male biased, as success would not be linked to knowledge of an area. However, females would need to invest more in protecting resources and therefore need better knowledge of an area.

Inbreeding depression results when close relatives inter-breed. Many studies have documented a significant decrease in the fitness of the progeny resulting from such matings (Ralls *et al.* 1979, 1988, Charlesworth & Charlesworth 1987). This decrease in fitness is due to both increased homozygosity, and therefore the increased exposure of deleterious recessive alleles, and to a loss of alleles, which will render a population less able to cope with environmental changes (Wilson 1975, Charlesworth & Charlesworth

1987, Barret & Charlesworth 1991). Outbreeding increases gene flow and therefore increases genetic variability and maintains genetic continuity in and between populations (Packer 1979, Pusey 1980, Pusey & Wolf 1996).

1.2 SOUTHERN ELEPHANT SEALS

1.2.1 Description

Elephant seals are members of the family Phocidæ and are thus true seals (King 1983). Two species are extant. These are of similar appearance and behaviour, and are separated mainly by range and timing of the breeding season (Bonner 1989, Ling & Bryden 1992). Northern elephant seals, *Mirounga angustirostris*, forage in the north-west Pacific ocean (De Long *et al.* 1992, Stewart & De Long 1994) and haul out to breed in the late boreal winter on islands off the coast of California and Baja California, and at a few colonies on the Californian mainland (Bartholomew & Hubbs 1960, Stewart *et al.* 1994).

Southern elephant seals, *M. leonina*, which are the subject of this study, inhabit the Southern Ocean, and breed in the austral spring. They are the larger of the two species, also being the largest of all species of pinnipeds (King 1983). Newborn pups weigh 40-46 kg and have a mean length of 1,27m. Adult males reach a mass of 3000 - 4000 kg and a length of 4,2 - 4,5 m. Adult females are much smaller, with a mass of between 400 and 900 kg and a length of between 2,6 and 2,8 m (Laws 1993). As indicated by their sexual dimorphism (Figure 1.1), females reach maturity much earlier than males. Most females first give birth at three to six years of age. Males generally breed for the first time from 7

Figure 1.1 Southern elephant seals, *Mirounga leonina*, at Marion Island during the breeding season. An adult male lies at the centre facing left, and in the foreground are an adult female and an unweaned pup.

to 10 years of age (Laws 1953, Carrick *et al.* 1962b, Jones 1981, McCann 1981), but at the site of this study they start breeding at younger age, generally from 6 to 8 years (Bester & Wilkinson 1994, Kirkman 1999, Pistorius *et al.* 1999).

1.2.2 Life history

The mating system is polygynous and the breeding season is highly synchronised. Mating associations are ephemeral, not being maintained beyond the breeding season. Adult females haul out at this time in aggregations known as harems (Figure 1.2) (Carrick *et al.* 1962a, Bonner 1989). These are often very dense and large, and harems consisting of up to 1000 females have been documented (Bonner 1989). During the period of this study at the study site, breeding aggregations rarely exceeded forty adult females (Wilkinson 1992). A single adult male, known as the beachmaster, dominates access to females. In the larger breeding aggregations sub-dominant males (assistant beachmasters) control access to females in restricted areas, but give way to the dominant male. This latter category does not occur at Marion Island (Wilkinson 1992). Also associated with the breeding aggregations are subordinate males (bachelors) which lie away from the females and which opportunistically mate with females that stray from the control of the dominant males, and subordinate males which are known to challenge beachmasters (challengers) (Laws 1956, Carrick *et al.* 1962a, McCann 1981, Wilkinson & Van Aarde 1999). The latter category occurs seldom on Marion Island and was only recorded once during the period of this study.

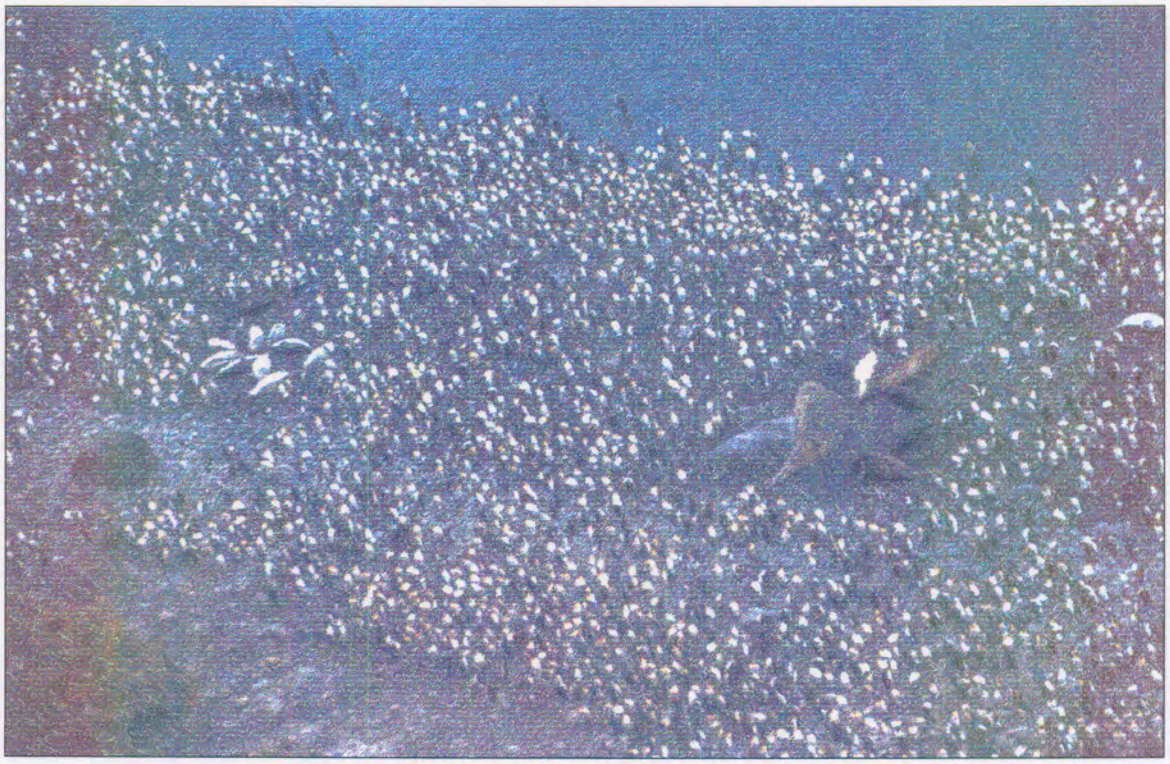

Figure 1.2 Groups of southern elephant seals, *Mirounga leonina*, at Marion Island during the breeding season, lying amongst king penguins, *Aptenodytes patagonicus*. On the right is a small breeding aggregation with a single adult male (the beachmaster), and three adult females and their dependant pups. On the left is an aggregation of recently weaned pups.

Southern elephant seals are predominantly marine, males spending approximately 30 % of their adult life on land, and females, approximately 15 %. These periods on shore, known as haulouts, are separated by trips of up to 8 months at sea (Carrick *et al.* 1962a, Hindell & Burton 1988, Wilkinson, 1992). During this time seals visit distant foraging grounds that may be several thousand kilometres from haulout sites (Bester & Pansegrouw 1992, Jonker & Bester 1998). As the seal hauls out twice a year, for reasons detailed below, it undergoes an annual double migration between haulout and foraging grounds (Carrick *et al.* 1962a, Hindell & Burton 1988, Wilkinson, 1992).

Elephant seals experience three types of haulout: (1) the winter haulout, (2) the annual moult, and (3) the breeding haulout (Carrick *et al.* 1962a, Condy 1979). In addition a fourth period ashore is experienced. This is the time from birth to a few weeks after weaning. During this period the seal pup will remain ashore for most of the time but may undertake short swims during which it either intentionally travels to, or be unintentionally carried to neighbouring beaches (Carrick *et al.* 1962a, Lenglart & Bester 1982, Wilkinson & Bester 1990).

The winter haulout is often referred to as the resting haulout (Carrick *et al.* 1962a, Condy 1979) but as the purpose of this haulout is uncertain, this term is not used. Although, it is theoretically more accurate to refer to this haulout as an autumn-winter haulout (Wilkinson 1992), this rather unwieldy term is also avoided. The winter haulout is experienced predominantly by immature animals, which haul out once or (for about 10 % of animals in this study) more than once per year between mid-January and mid-September (Wilkinson 1992, Kirkman 1999).

All elephant seals haul out annually to moult between the end of October and April. This haulout lasts for approximately one month. Mature animals haul out to moult later than immature animals, and adult males later than adult females (Carrick *et al.* 1962, Kirkman 1999).

Adult southern elephant seals haul out to breed during the austral spring. Adult males arrive at their breeding site from late August and spend periods of one to three months ashore. Adult females haul out for approximately one month in September or October. They give birth to their pups about three days after coming ashore and suckle them for the next three weeks. Shortly before the adult females return to sea they mate with the adult males (Laws 1956, Carrick *et al.* 1962a, Condy 1979).

During their lifetime elephant seals will therefore experience a typical pattern of periods ashore. As a newborn pup it will remain ashore for a few weeks after weaning. As an immature it will alternate between winter and moult haulouts, and as an adult it will alternate between breeding and moult haulouts (see Appendix 6).

1.2.3 Distribution

Southern elephant seals inhabit the Southern Ocean between about 40°S and the Antarctic Continent (Figure 1.3). Most haulout sites are on subantarctic and Antarctic islands but the seals also regularly haul out at sites on the coasts of South America (Campagna & Lewis 1992) and Antarctica (Murray 1981, Bester 1988). Occasional vagrants have been recorded on the coasts of Southern Africa (Oosthuizen *et al.* 1988), Tasmania and New Zealand (Taylor & Taylor 1989).

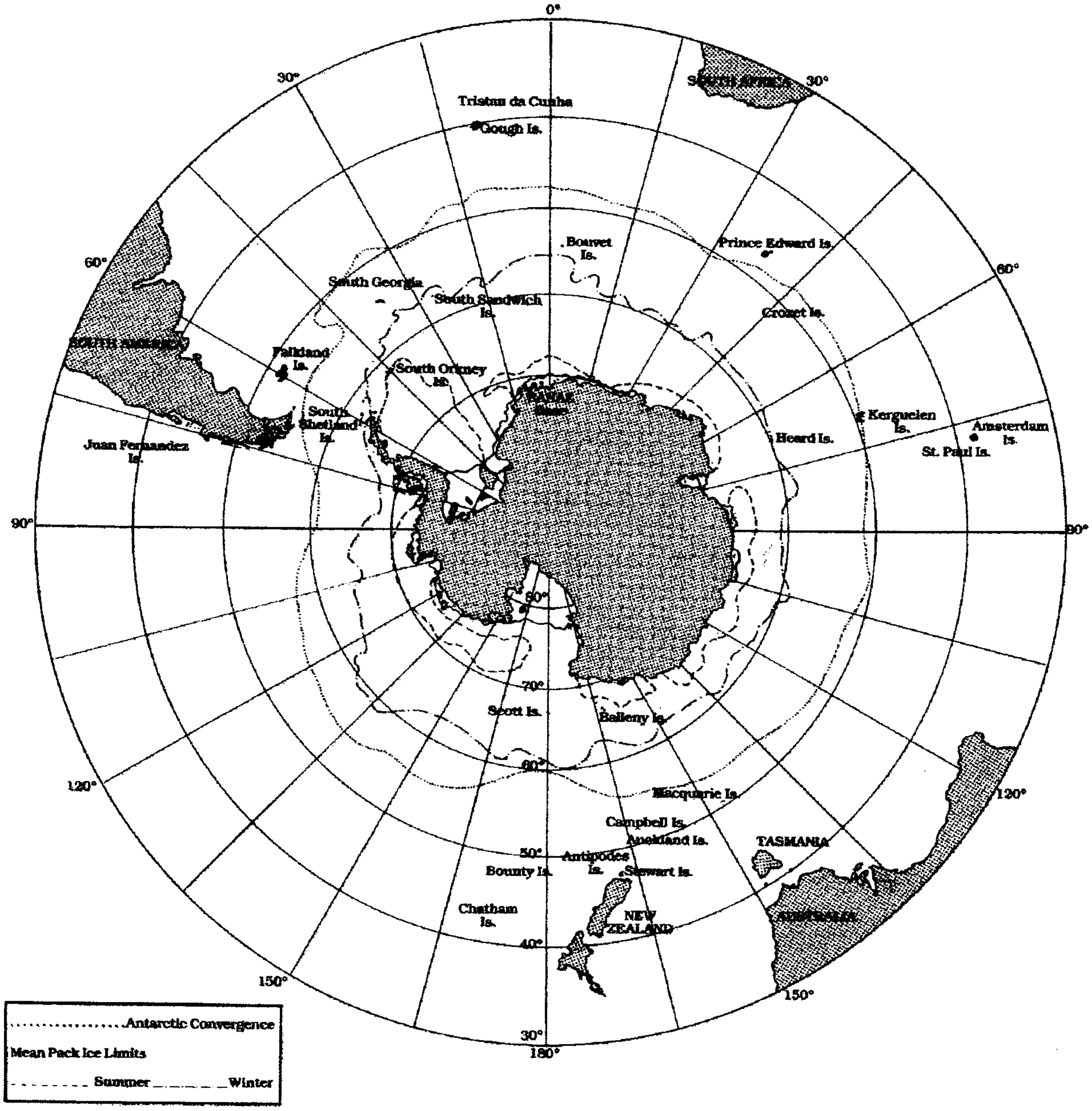

Figure 1.3 The locations of southern elephant seal, *Mirounga leonina*, haulout sites mentioned in Table 1.1. The study site, Marion Island, is one of the two islands of the Prince Edward Island Group.

The population structure of southern elephant seals is detailed in Table 1.1. The world population of about 750 000 individuals (McCann 1985) has been separated into three major regional populations or "stocks" (the South Georgia, Macquarie, and Kerguelen stocks) (Laws 1960) between which there is apparently very little movement of individuals and consequently genetic isolation (Gales *et al.* 1989, Hoelzel *et al.* 1993, Wynen *et al.* submitted). Following metapopulation theory each of these stocks could be described as a metapopulation (Hanski & Gilpin 1991). Each stock consists of a number of breeding populations of varying sizes, each associated with an island or a group of islands, and separated from other like populations by distances of between 400 and 3000 km. The South Georgia Stock includes populations at South Georgia, Peninsula Valdés, the Falkland Islands, the South Shetland Islands, the South Orkney Islands, Gough Island and Bouvetøya. Breeding populations in this stock may also exist on the South Sandwich Islands. The Kerguelen stock includes populations at the Iles Kerguelen, Iles Crozet, Heard Island and the Prince Edward Islands, and the Macquarie stock includes the Campbell Island, Auckland Island and Antipodes Island populations (Laws 1960). Some populations can be further divided into subpopulations of separate islands within an island group, which may be separated by distances of up to 100 km (Guinet *et al.* 1992). On each island seals may breed at a number of sites, usually on isolated beaches, and each of these beaches may contain a number of independent breeding aggregations. It is the movement between these sites that is the subject of this study.

Table 1.1 Estimated pup production of island populations of southern elephant seals, *Mirounga leonina*.

Stock	Island/Island group	Estimated pup production	Year of estimate	Reference
South Georgia	South Georgia Is.	113 444	1995	Boyd *et al.* 1996
	South Orkney Is.	< 100	1985	McCann 1985
	Bouvetøya	89	1998	Kirkman *et al.* 2000
	Falkland Is.	Approx. 1000	1960	Laws 1960
	Sea Lion Is. (Falklands)	535	1999	Galimberti (pers.comm.) in SCAR 2000
	Gough Is.	18	1998	Bester (pers.comm) in SCAR 2000
	King George Is. (S. Shetland Is.)	301	1999	Carlini (pers.comm.) in SCAR 2000
	Nelson Is. (S. Shetland Is.)	106	1985	Vergani *et al.* 1987
	Peninsula Valdés	13 655	1999	Lewis *et al.* 1998
Kerguelen	Marion Is.	425	1999	Bester (pers.comm.) in SCAR 2000
	Heard Is.	17 – 18 000	1992	Slip & Burton 1999
	Courbet Peninsula (Iles Kerguelen)	43 000	1997	Guinet *et al.* 1999
	Ile de la Possession (Iles Crozet)	570	1997	Guinet *et al.* 1999
Macquarie	Macquarie Is.	19 737	1999	Burton (pers.comm.) in SCAR 2000
	Campbell Is.	5	1986	Taylor & Taylor 1989
	Antipodes Is.	113	1978	Taylor & Taylor 1989

Based on Table 3.3 in SCAR (2000)

1.3 A REVIEW OF DISPERSAL AND DISPERSION IN PINNIPEDS

Pinniped dispersal and dispersion have received little attention because of the difficulties associated with the studies of animal movements, and of marine mammals. Projects addressing the problems of dispersal require the identification of large groups of individuals and the regular observation of their movements over long periods of time (Caughley 1977). Pinnipeds pose their own research problems by virtue of their predominantly marine life history and the inaccessibility of many of their haulout sites (King 1983).

Past studies of seal movements have relied on the following sources of information:

1. Sightings of unmarked individuals either within or outside of (vagrants) their main range,
2. Movements of individuals carrying VHF transmitters,
3. Movements of individuals carrying satellite-linked platform transmitter terminals (PTTs), also known as satellite tags, and geolocation time-depth recorders (GLTDRs),
4. Genetic studies,
5. Sightings of brand-marked, tagged or collared individuals.

Reports of vagrant seals are common for both otariids and phocids. Vagrant otariids have been reported for Subantactic fur seals, *Arctocephalus tropicalis* (Payne 1979, Shaughnessy & Ross 1980, Torres & Aguayo 1984, Carr *et al.* 1985, Bester 1989, Goldsworthy & Shaughnessy 1989, David *et al.* 1993), Antarctic fur seals, *A. gazella* (Payne 1979), Cape fur seals, *A.pusillus pusillus* (Kerley 1983), and Northern fur seals, *Callorhinus ursinus* (Griben 1979), amongst others. Vagrant phocids reported include Mediterranean monk seals, *Monachus monachus* (Boutiba 1990, Maigret 1990), hooded seals, *Cystophora cristata* (Ibáñez *et al.* 1988, Dudley 1992), harp seals, *Phoca grœnlandica*, (McAlpine & Walker 1990), and leopard seals, *Hydrurga leptonyx*, (Bester & Roux 1986, Slater 1991, Rounsevell & Pemberton 1994). Although these reports may indicate the extension of ranges (Shaughnessy & Goldsworthy 1990) and maximum distances of movement possible, the information is too limited to allow conclusions concerning the characteristics of dispersal.

Recorded movements of seals carrying VHF transmitters (e.g. Thompson *et al.* 1994a), satellite-linked PTTs (Stewart *et al.* 1996) or GLTDRs (e.g. Hindell *et al.* 1991, Stewart & De Long 1992, 1995, McConnell & Fedak 1996, Jonker & Bester 1998) indicate movements in great detail, but of relatively few individuals. These devices cannot be applied to large groups of seals or for long periods of time due to their expense, the practical problems encountered in deploying them and their limited memory. Therefore, they cannot indicate the proportion of a population that disperses, nor specify which age and sex classes, nor the extent of dispersal. Such devices only give an idea of the possible origins and destinations of a population, or the movements of very few individuals. For a study of dispersal such data are inadequate.

Genetic studies have compared the populations of a number of species of seal, such as Antarctic and Subantarctic fur seals, (Wynen *et al.* 2000), the New Zealand fur seal, *Arctocephalus fosteri* (Lento *et al.* 1994), the Guadelupe fur seal, *A.townsendi*, (Bernardi *et al.* 1998) the California sea lion, *Zalophus californianus*, (Maldonaldo *et al.* 1995), the Weddell seal, *Leptonochytes weddellii*, (Shaughnessy 1969), and the grey seal, *Halichœrus grypus*, (Amos *et al.* 1995). These studies are able to show the past mixing of populations (Lento *et al.* 1994) and the relationship between individual seals (Amos *et al.*

1995). They do not, however, indicate the proportions of various classes of seals moving and the factors affecting these movements. Genetic studies also relate primarily to the past movements of animals, not to current movements (Avise *et al.* 1992).

Marking studies can provide volumes of useful information if conducted correctly. Such studies require marking of animals soon after birth (so that known-aged cohorts are marked at their natal site), the marking of large groups of individuals (whole populations, if possible) and regular and systematic resighting at all possible haulout sites. Animals are marked using tags, brands or scar marks (Reviewed in Erickson *et al.* 1993) and collars (Chelnokov 1970 in Griben 1979). Future studies of dispersal may make use of individual genetic tags (Palsbol *et al.* 1997).

The dispersal of pinnipeds has been the subject of only one review, that by Baker (1978). He considered 12 species of seals, for only three of which, the northern fur seal, the Cape fur seal and the grey seal, were data from marking studies available. For the other species he inferred dispersal from sightings of vagrants, seasonal population movements and the observation of new colonies. Data on dispersal and dispersion were summarised by Riedman (1990) in a table dealing with migration in all species of pinnipeds.

1.3.1 Otariids

Among the most studied of otariids are northern fur seals. Large numbers have been tagged at the four major population centres, these being the Pribilof (Kenyon 1960, Griben 1979), Commander, Kuril and Robben Islands (Aschepkov & Kuzin 1987). Seals move between all four of these populations (Griben 1979, Aschepkov & Kuzin 1986,

1987) and to the more distant and smaller San Miguel Island population (Peterson *et al.* 1968).

Philopatry has been shown for female northern fur seals at the Pribilof Islands (Kenyon 1960, Baker *et al.* 1995). Females typically haul out to breed within metres of the actual site at which they were born or had previously pupped (Bartholomew 1953 in Kenyon 1960, Chelnokov 1982 in Baker *et al.* 1995). Fidelity increased significantly with age: 82% of ten-year-old females at St. Paul Island that hauled out, did so at their natal area, whereas the proportion of two-year-olds was only 65%. Similar haulout patterns were shown for males, although they were significantly less philopatric (Baker *et al.* 1995). The authors suggested that this was due to the greater age at which males attained sexual maturity. Females were already breeding at three years of age, whereas males remained subadults until seven years of age.

A number of other studies by the North Pacific Fur Seal Commission and the Marine Mammal Division (Reviewed in Griben 1979) indicate that most seals moving between islands are immature individuals. Of these, some breed on the islands to which they have transferred (Peterson *et al.* 1968). In the Pribilof group, 13 – 14 % of subadult males moved between the two major islands (Griben 1979). It is not known, however, how permanent these transfers are, nor the proportion of individuals that breed in populations other than their natal ones.

Although the movements of Antarctic fur seals have received far less attention, they have also been shown to be philopatric. At least 65% of adult females return to breed at the same beach in successive years. As with Northern fur seals, females hauled out close to the actual position on the beach on which they had pupped previously (Lunn & Boyd 1991).

Oosthuizen (1991) addressed the dispersal of Cape fur seals. The sexes were found to disperse equally and most animals found at some distance from their natal site were immatures. As these animals aged they became increasingly philopatric, and many of them may have therefore returned to their natal colonies to breed. The establishment of new colonies and the enormous increase in the size of others, however, indicate that at least some seals must breed at new colonies. Evidence from another study (Rand 1959) indicates that at least some females show fidelity to previous pupping sites. Breeding philopatry has also been indicated for New Zealand fur seals (Stirling 1971) and South American fur seals, *A. australis* (Harcourt 1992). These studies did not, however, address other aspects of site fidelity.

Of the sea lions, philopatry has only been observed in the Californian sea lion, though it likely occurs in other species. Ridgway & Robison (1985) noted that sea lions that were moved to other sites 115 to 240 km distant, returned to their capture sites within four days.

Genetic studies have yielded further information on philopatry and dispersal in fur seals. Data from a study by Shaughnessy (1970) indicated dispersal between various Australian fur seal populations in Victoria and Tasmania. He also indicated that dispersal of New Zealand fur seals from New Zealand might have been responsible for repopulating possibly extinct colonies of this species at Macquarie Island and in South and West Australia. Lento *et al.* (1994) contradicted these conclusions. They found genetic differences between populations of New Zealand fur seals in New Zealand and West Australia, suggesting that few individuals moved between the two populations. Wynen *et al.* (2000) found little intra-specific genetic distinction between various populations of both Antarctic and Subantarctic fur seals. Their findings did, however, suggest some geographic lineages, with some populations descended from colonisers from certain other populations. Genetic studies of Californian sea lions indicate that the population from the Gulf of California is isolated from the population of the Pacific coast of North America (Maldonaldo *et al.* 1995). However, the same studies indicate movement of breeding individuals between colonies within the latter population. The authors suggested that Californian sea lions were philopatric to their region but not necessarily to their colony.

1.3.2 Phocids

One of the most studied of the Phocidæ, with respect to dispersal is the Weddell seal population of the Ross Sea, Antarctica. Large numbers of pups have been tagged since 1963 (Stirling 1969, Testa 1987b). These studies have shown very little breeding dispersal (Stirling 1969, 1974, Testa 1987b) but relatively high natal dispersal (Testa 1987a & b). The majority of adult females bred at the colony at which they had pupped in the previous year, or at the colony closest to it (Stirling 1969). Dispersers were predominantly pups, subadults, and young adult females (Stirling 1974, Testa 1987a). Dispersal between sub-populations of the Ross Sea shown by Testa (1987b) is supported by genetic evidence (Shaughnessy 1969).

A study of Weddell seals at the Signy Islands confirmed these findings. Older adult females were found to be highly philopatric while younger adult females and subadults dispersed more readily. This population was also not discrete and seals born on Signy Island bred on other islands in the South Orkneys (Croxall & Hiby 1983). Unfortunately none of these studies indicate the degree of dispersal of male Weddell seals.

A number of studies of grey seal movements have been completed, the majority of which made use of tagging. Most tag recoveries were of juvenile seals (Bjørge & McConnell 1986). These showed that, although the majority of young seals remained within 100 km of their birth site, a substantial number moved farther afield, the furthest recorded movement exceeding 1000 km (Wiig & Øien 1987). Movements between most populations in Europe have been recorded, but it is possible that most seals taking part in these movements return to their natal populations (Baker 1978). Nevertheless, the fact that new colonies have been formed show that at least some of these movements must result in dispersal (T'Hart *et al.* 1988).

Other studies have shown site philopatry in adult female grey seals. Adult females seldom change their pupping sites from year to year. In a study on the Island of Rhona, Scotland, 93% of adult females returned to breed at sites at which they had pupped in previous years (Pomeroy *et al.* 1994). One seal, however, pupped 160 km from her previous pupping site. Most seals that pupped at their preferred haulout beach did so within metres of their previous pupping site (Boness & James 1979, Pomeroy *et al.* 1994). Anderson *et al.* (1975) and Pomeroy *et al.* (1994) found that some females moved several times before settling at their pupping site. Genetic work has provided evidence for philopatry in grey seals, showing that adult females not only show fidelity to previous pupping sites but also to mates (Amos *et al.* 1995).

Studies of common or harbour seals (*P. vitulina*) indicate that they are fairly sedentary seals, few of them travelling far from their natal sites (Bonner & Withames 1974). Dispersal does occur, however, with some individuals found as far as 500 km from their tagging site (Bonner & Withames 1974, Thompson *et al.* 1994b). As with other species most of those individuals that dispersed were immatures (Thompson 1989). Studies using VHF tags have indicated that adult seals travel directly between feeding areas and haulout sites. They also show that these locations are within 29 - 46 km of one another (Thompson & Miller 1990, Thompson *et al.* 1994a).

Leopard seals are little studied and knowledge of their dispersal is limited to movements of vagrant individuals, which show that dispersal is generally seasonal (Bester & Roux 1986, Borsa 1990, Rounsevell & Pemberton 1994). Most of these vagrants are immature animals (Borsa 1990, Rounsevell & Pemberton 1994). Rounsevell & Eberhard (1980) suggested that at least some individuals showed fidelity to haulout sites.

In common with other seals, hooded seals also experience predominantly juvenile dispersal. While individuals do not move far shortly after weaning, they disperse further with age. Individuals tagged on islands off the Atlantic coast of Southern Canada moved as far as France (Hammil 1993). Studies indicate, however, that there is little mixing between individuals of different breeding populations (Hammil 1993).

Baikal seals, *P. sibirica*, are limited to Lake Baikal, and show seasonal migration between the northern and southern ends of the lake (Stewart *et al.* 1996). Individuals seem to return to areas used in previous seasons (Pastukhov 1990 in Stewart *et al.* 1996).

1.3.3 Elephant seals

Unmarked vagrant elephant seals have been recorded a number of times (Best 1971, Heimark & Heimark 1986, Ingham 1957, Kettlewell & Rand 1955, Mills *et al.* 1977, Murray 1981, Oosthuizen *et al.* 1988, Taylor & Taylor 1989). Although these sightings are of limited use they do indicate that elephant seals are capable of moving vast distances. The greatest recorded distance travelled by an elephant seal was that of a yearling of the northern species captured on an island off the East coast of Japan, 11 000 km west of the nearest breeding colonies across the Pacific ocean (Kiyota *et al.* 1992). The furthest recorded distance moved by a southern elephant seal was that of an adult female shot on the coast of the Sultanate of Oman in the North Arabian Sea. The closest breeding population is that on the Iles Crozet 9 000 km to the South (Johnson 1990). Although most vagrants are merely individuals that have drifted far from their regular haulout sites (Oosthuizen *et al.* 1988, Taylor & Taylor 1989), some have been recorded to breed at the sites at which they are found, indicating a possible extension of range (Heimark & Heimark 1986, Ingham 1957, Kettlewell & Rand 1955, Mills *et al.* 1977, Murray 1981). These records therefore indicate that elephant seals are capable of dispersing vast distances, and that dispersing animals may have been responsible for the inception of new colonies.

Recorded long distance movements of tagged individuals are of greater interest, as their site of origin is known. The furthest distance travelled by such an individual is 5200 km by a seal which had been branded as a newly weaned pup on Macquarie Island. It was recorded 16 months later on Peter I Øy, Antarctica (Hindell & McMahon 2000). Other movements exceeding 4 000 km have also been recorded (Vaughan 1967, Slip *et al.* in press). Such records also indicate the amount of movement, and possible dispersal, between populations (Bester 1988, 1989, Burton 1985, Guinet *et al.* 1992, Slip *et al.* in press).

Movements of elephant seals have been recorded by GLTDRs and PTTs in a number of studies. Most of these indicate movements to foraging grounds rather than movements between different haulout sites. Male northern elephant seals migrate to areas in the northern Pacific as far as the Aleutian Islands, 2000 km distant. Females of this species travel distances of up to 1900 km from regular haulout sites (De Long *et al.* 1992, Stewart & Delong 1992, 1995). Male and female southern elephant seals migrate similar distances to areas in the Southern Ocean as far from their breeding grounds as the Antarctic Continent (Hindell *et al.* 1991, Jonker & Bester 1998, McConnell & Fedak 1996).

While no published studies of northern elephant seals have specifically addressed dispersal, a number have noted it. Huber *et al.* (1991) recorded relatively high natal dispersal, but practically no breeding dispersal by females of the South Farallon Islands, California, population. Of females surviving to breed, 15 % pupped for the first time on islands other than their natal island. However, almost no females reproduced on an island other than the one on which they had first pupped. Immigration to the South Farallon Islands and to Isla Año Nuevo was mostly by young females from island groups closest to the study islands (Reiter *et al.* 1981, Huber *et al.* 1991). The number of immigrants to the South Farallons from neighbouring islands was proportional to the distance between the islands (Le Boeuf *et al.* 1974, Huber *et al.* 1991).

No studies have compared dispersal between beaches of the same island for northern elephant seals, but Stewart (1989) noted that younger females tended to move away from densely populated harems.

Studies that use individually marked southern elephant seals and that incorporate observations of dispersal and other movements, have been conducted at five sites; Macquarie Island, Iles Kerguelen, Peninsula Valdés, Vestfold Hills and Marion Island. The most extensive of these are of the population on Macquarie Island. Large numbers of seals have been branded at this site and some resighted over a number of years. The earliest observations indicated that females returned to breed near or at their birth site (Carrick & Ingham 1962a) and were more philopatric than males (Carrick & Ingham 1962b). Hindell and Little (1988) recorded philopatry by females of over 20 years of age. A study by Nichols (1970) showed that greater distances were moved in dispersion than in dispersal. A large majority of seals hauled out at their natal site during the breeding season. Seals were, however, more evenly spread over the island's beaches during the moult and the winter haulout. No age differences in dispersal were evident but females were more philopatric than males. Some 77% of adult females hauled out within 4 km of their natal site during the breeding season, whereas only 60% of males did so. During the moulting season only young adult females showed a significant degree of philopatry. All other age and sex classes showed even dispersion (Nichols 1970).

A study of elephant seals on Iles Kerguelen (Bester & Van Niekerk 1984) described the effects of age, sex and habitat on dispersal and dispersion. Adult females were found to show a high degree of site fidelity during the breeding season. During the moult the dispersion of seals was influenced by the location of preferred habitat. Immature seals dispersed further than adults during the moult. No difference in dispersion between the sexes was found in immatures, but adult males moved further than adult females. A considerable proportion of adult seals moved between moulting areas during a single moulting season. In another study at Iles Kerguelen, Lenglart & Bester (1982) considered the dispersion of under-yearlings shortly after weaning. The movement of individuals along the coast before their first extended trip to sea was largely dependent on prevailing wave and wind direction. No significant difference in dispersion between the sexes was found.

The population of elephant seals at the Peninsula Valdés is more widely spread out than most, being found over a coastline of 200 km in length. A large number of seals have been marked at their natal sites or when they hauled out as adults. Campagna & Lewis (1992) found individuals breeding or moulting 100 km or further from their natal site. They believed that this indicated that seals from this location showed less site fidelity than others by virtue of the dispersed nature of their population. More recent data have shown, however, that although a few seals haul out as far as 120 km from their marking sites, most breed and moult close to their marking sites (Lewis *et al.* 1996). While some individuals also moult on the Falkland Islands, over 1000 km away, none have been recorded breeding amongst the local population (Lewis *et al.* 1996, Galimberti & Boitani 1999).

The Vestfold Hills, Antarctica, are used as a moult site, primarily by subadult and adult male southern elephant seals (Tierney 1977). These seals were born at the Iles Kerguelen and Heard Island, and presumably return to breed there (Bester 1988, Burton 1985).

Despite this individuals show fidelity to their moult sites. Approximately 40% of tagged seals moulting at the Vestfold Hills return in later years (Gales & Burton 1989).

The post-weaning dispersion of elephant seal pups has been the focus of several studies at Marion Island (Panagis 1981, Wilkinson & Bester 1990). Little dispersion took place between weaning and departure for the first pelagic phase. However, movement between beaches did increase with time after weaning. In contrast to post-weaning dispersion at Iles Kerguelen (Lenglart & Bester 1982), Wilkinson & Bester (1990) found sex-related differences, with males being the predominant and most adventurous dispersers.

1.4 NULL HYPOTHESES

Despite the number of studies on dispersal and dispersion in pinnipeds, much remains unknown, especially compared to terrestrial animals. An extensive and detailed database exists, covering a period of more than ten years, of the movements of individually marked animals at Marion Island. This has presented the opportunity to pursue a number of questions, including: Do these seals show any fidelity to their natal site and first breeding site? Is there any difference between natal dispersal, breeding dispersal, moult dispersion or winter dispersion? Do male or female seals show greater site fidelity? Do any characteristics of the seals themselves, or of their natal environment affect dispersal? To address these questions the validity of the following hypotheses is tested:

1. The seals do not haul out closer to their natal or first reproductive site than would randomly be expected.
2. There is no difference between any types of either dispersal or dispersion.
3. There is no sex bias for any type of dispersal or dispersion.

4. None of a number of factors related to a seal's birth or natal environment has any effect on any type of dispersal and dispersion.

Within each of these hypotheses a number of sub-hypotheses are investigated. These are noted below.

1. Southern elephant seals at Marion Island do not haul out closer to their natal or first reproductive site than would randomly be expected.

Neither male nor female seals haul out any closer than expected:

1.1 to their natal site to reproduce,

1.2 to their natal site to reproduce for the first time,

1.3 to their first reproductive haulout site to reproduce again,

1.4 to their natal site to moult,

1.5 to their natal site to winter.

2. There is no difference between any types of either dispersal or dispersion for southern elephant seals at Marion Island.

There is no difference, for either males or females, between any of the following types of dispersal or dispersion:

2.1 natal and breeding dispersal,

2.2 distances displaced from natal site and from first reproductive haulout site during later reproductive haulouts,

2.3 moult and winter dispersion,

2.4 all dispersal and moult dispersion,

2.5 all dispersal and winter dispersion.

3. There is no sex bias for any type of dispersal or dispersion by southern elephant seals at Marion Island

No sex bias is shown in:

3.1 all dispersal,
3.2 natal dispersal,
3.3 breeding dispersal,
3.4 moult dispersion,
3.5 winter dispersion.

4. No factor related to a seal's birth or subsequent growth has any effect on any type of dispersal and dispersion by southern elephant seals at Marion Island.

The following factors have no effect on dispersal or dispersion of male or female seals:

4.1 cohort,
4.2 age,
4.4 natal site isolation,
4.5 human disturbance of natal harem,
4.6 natal harem size,
4.7 pre-weaning mortality.

This study therefore seeks to describe the characteristics of dispersal and dispersion in southern elephant seals at Marion Island. It does not detail the reasons for the characteristics evident, but rather speculates as to what they may be, and proposes further questions that would need to be answered to fully elucidate the long-term movements of these animals.

CHAPTER 2

STUDY SITE

2.1 LOCATION

Marion Island (46°54'S, 37°45'E) is one of two islands found in the Prince Edward Island group, the other being Prince Edward Island itself. The islands are separated by 22 km but are similar in topography, climate and the composition of species that they support. The group is situated in the Southern Ocean, 2300 km south east of the African Continent and 2100 km north of Antarctica (Figure 1.3). The islands are relatively isolated, the nearest land being the Crozet Islands, 1050 km to the East. Marion is the larger of the two islands with an area of 290 km^2, and a circumference of 90 km. Prince Edward Island is only 80 km^2 in area (Verwoerd 1971).

2.2 TOPOGRAPHY

The Prince Edward Islands are of recent volcanic origin and are rugged both in appearance and form. Marion Island slopes from a central mountainous highland with an altitude of over 1000 m to a coastal plane. The coast is irregular in form and mostly formed by cliffs of between 15 and several hundred metres in height. These cliffs are broken in a number of places by rough beaches (Appendix 3) and it is on these that elephant seals haul out. Most of the beaches lie on the sheltered northern and eastern coasts, between sites known as Cape Davis and Kildalkey Bay (Figure 2.1). However,

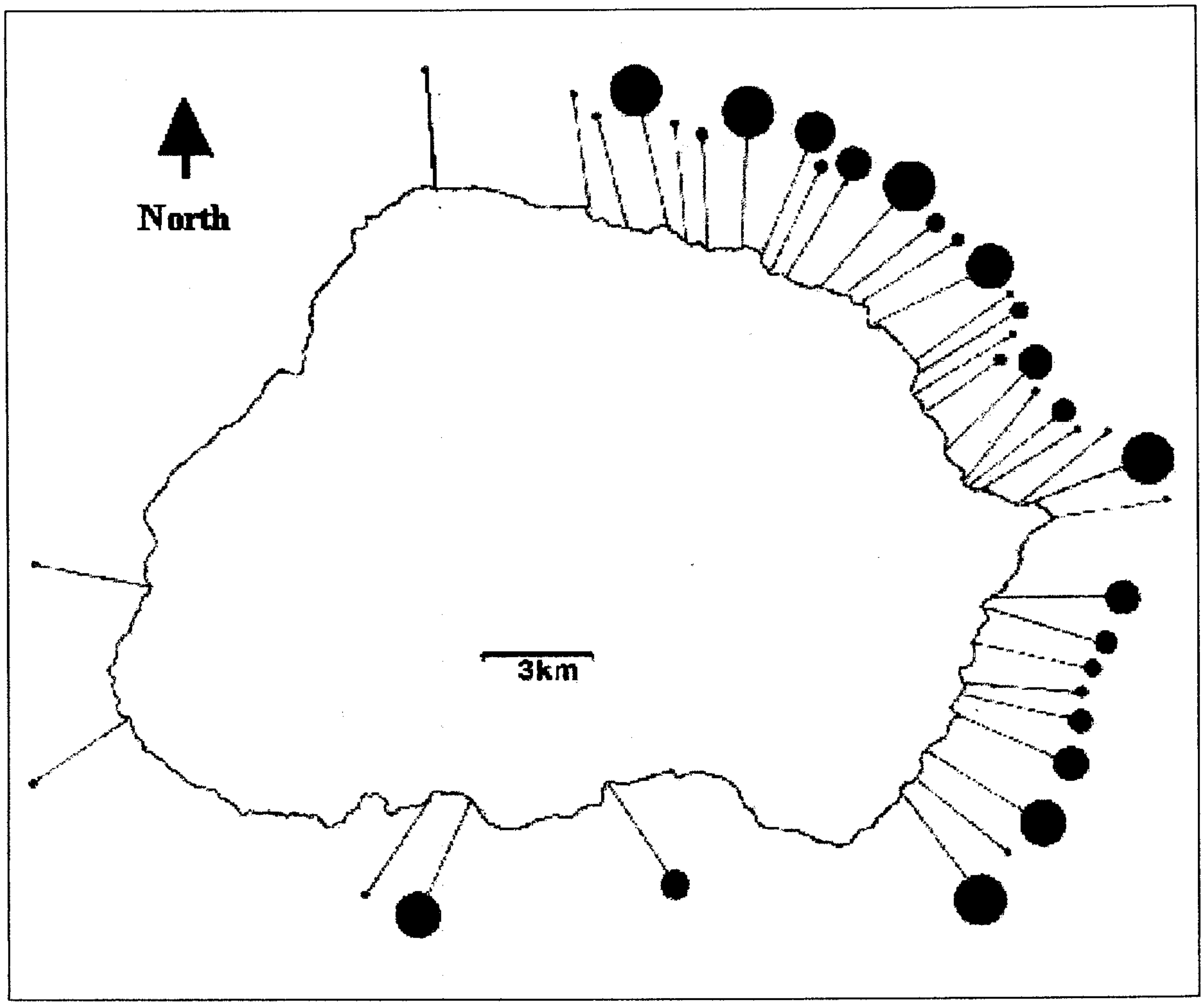

Figure 2.1 An outline of Marion Island, showing the distribution of southern elephant seal, *Mirounga leonina*, breeding localities. The area of each circle is proportional to the number of seals tagged as pups at each site from 1983 to 1994.

two relatively isolated beaches, also of importance to elephant seals, lie on the South Coast at Watertunnel Bay and Goodhope Bay East. Pebbles and small boulders form the substrate of most of the beaches, there being only one sandy and one shingle beach on the island. Elephant seals breed and rest on these pebble, boulder, sandy or shingle areas and moult in the tussock grass and mud wallows that are found at the back of most beaches (Condy 1979).

2.3 CLIMATE

The climate of Marion Island is largely determined by its latitude and isolation. At 46°S it lies within that zone of the Southern Ocean known as the "Roaring Forties", and at over 2000 km from the nearest continent, it is subject to a subantarctic and an oceanic regime. The climate is ameliorated to some extent, due to the 230 km distance between it and the Antarctic Polar Front to the south. The climate varies only slightly both seasonally and diurnally. Major features include low temperatures (annual mean of 5°C), high annual precipitation (2576 mm annually) and strong sustained westerly winds with frequent gales. The island is also subject to high humidity and a high degree of cloud cover (Schulze 1971).

CHAPTER 3

METHODS

3.1 DATA COLLECTION

The data used in this thesis were collected over 12 years (from November 1983 to November 1994), as part of a long-term study conducted on Marion Island during which southern elephant seals were regularly tagged and resighted. The coastline of the island was divided into 68 potential haulout sites (i.e. beaches or sections of the coastline) (see Figure 3.1 and Appendix 3) and the limits of each of these sites were defined (Mammal Research Institute 1987). That part of the island with sites more commonly visited by southern elephant seals, was denoted the Extended Study Area.

Southern elephant seals at Marion Island have been regularly tagged since 1973. Prior to 1983 monel metal tags were used. Since 1983 the vast majority of seals born on the island have been tagged with plastic Dal 8 Jumbo Rototags (Dalton Supplies (Pty.) Ltd., Henley-on-Thames, England. Seals were tagged as pups within days of weaning and therefore at their site of birth (Wilkinson & Bester 1990). Each pup was double tagged in the interdigital webs of each hind flipper, between the second and third, or the third and fourth digits (Figure 3.1). Tags were colour coded for the year in which a seal was born and were engraved with a number unique to the seal in its cohort. Each seal born on the

Figure 3.1 One of the hind-flippers of an immobilised eight-year-old male elephant seal, *Mirounga leonina*, showing the placement of a tag.

island could therefore be individually identified. Seventeen sites, at which more than 90 pups were tagged between 1983 and 1994 (12 breeding seasons), were denoted major parturition sites. Other sites were neither popular, nor regularly used during the breeding season.

Resighting of seals before 1983 was irregular. From November 1983 a programme of regular resighting was instituted. From that date beaches on the northern and eastern sections of the coastline were visited every 7-10 days, and the southern beaches, at least once a month, between September and May each year. Since 1990, beaches were visited throughout the year, following the same pattern, and since September 1992 the southern beaches were also visited every 7-10 days.

Resightings were completed by one or two observers who visited all the beaches in the extended study area over a period of 2-3 days. During each resighting census the following data were recorded separately for each site:

1. The number of seals of each age and sex category,
2. The number of seals with tags,
3. The tag number for each tagged seal,
4. The number of tags borne by each seal,
5. The social status and moulting condition of each tagged seal.

3.2 THE DATABASE

3.2.1 Data available

The database consists of a number of records. Each is a single observation of a tagged seal on a specific date at a specific location, with all the category and natal environment data relevant to that seal for that observation. The following data are included in the database:

Location data for each seal:

1. Date and site of tagging,
2. Date and site of all sightings of pups prior to their first extended period at sea,
3. Date and site of all breeding season sightings of adults,
4. Date and site of all moulting season sightings,
5. Date and site of all winter sightings.

Category data:

1. Sex,
2. Age at each haulout,
3. Cohort,
4. Type of reproductive behaviour during each reproductive haulout sighting,
5. Stage of moult during each moult haulout sighting.

Natal environment data:

1. Natal harem size,
2. Natal harem pre-weaning mortality,

3. Natal site isolation,
4. Natal harem disturbance.

Dispersal and dispersion were measured in terms of the distances between two sites. Except for breeding dispersal, this was the distance between natal site and the later haulout site noted in each case. For breeding dispersal this was the distance between the first reproductive haulout sites and subsequent reproductive haulout sites. All distances were measured along the curve of the coastline from the middle of one site to the middle of the next. All animals tagged and resighted were presumed to be located at the middle of the site at which they were recorded.

Data were defined or determined as follows (where not detailed above or where not obvious):

Age: The chronological age of a seal in years. A seal became a year older at the beginning of a breeding haulout, or on the 15th of October.

Cohort: The year in which the seal was born from 1983 to 1993.

Type of reproductive behaviour: Females were recorded as pre-parturient, lactating with pup, or hauled out only for mating. Males were recorded as either beachmasters or bachelors (the latter category including challengers).

Natal harem size: The number of pups born at the natal site in the natal year.

Pre-weaning mortality: The percentage of pups born at a site that died prior to weaning, from 1990-1994 (five seasons).

Natal beach isolation: The distance from a site to the nearest Major Parturition Site, that is, a site at which at least 90 pups were born from 1983 to 1994.

Natal harem disturbance: A relative measure of the degree of human disturbance to which a harem was exposed. Harems exposed to high levels of disturbance were at sites close to the scientific station (within 4,3 km.) and commonly visited two or more times per week. Harems exposed to a medium level of disturbance were commonly visited once every 7-10 days. Harems exposed to low disturbance were visited about once a month, and harems that were visited less often than this were exposed to very low levels of disturbance. (See Appendix 3.)

3.2.2 Selection of records

The dataset analysed was restricted to records of the eleven cohorts born from 1983 to 1993, and collected from November 1983 to August 1994 in the case of immature seals and November 1983 to November 1994 in the case of adults. This dataset comprised 33 167 records from which 153 records of 54 individuals of unknown sex were removed leaving a total of 33 014 records of 5700 individuals.

Elephant seals were often recorded several times during one haulout event, sometimes at different sites. This study is concerned with movements between haulout events, and not the relatively minor movements between sites during a haulout event, the analysis of which encompasses sufficient scope for another study. It was assumed that a seal used one site during each haulout event to accomplish the purpose of that haulout and that other sites visited are not relevant for the purpose of discussing dispersal and dispersion on this scale. This is a reasonable assumption for natal haulouts, since a pup obviously cannot be born in more than one place, and also for breeding haulouts by females, which are restricted to a single site by the immobility of their pup, and moult haulouts, where animals usually show some aversion to entering the sea (pers. obs.). Animals hauling out during the winter, however, and more especially, males hauling out during the breeding haulout by males, may visit more than one site during that haulout event to accomplish their purpose. A single haulout record, termed the primary haulout record, was therefore selected to represent each haulout event. A total of 17 231 primary haulout records were selected. These were selected on criteria noted below.

Natal "haulout" event: The first record for each seal (when it is tagged) and which is at the site at which it was born, was retained as the record of its birth. Although this is technically not a haulout, since the animal arrived at the site by being born there, it is referred to as a haulout event as a form of shorthand. Not included in this category were all post-weaning records of haulouts by underyearlings prior to their first extended period at sea, which were eliminated from the database. Total natal haulout events: 5 700.

Reproductive haulout event: The first record of the main breeding site was retained as the primary record for each reproductive haulout event. For females the main breeding site was the pupping site, or if pupping was not recorded, the most frequently recorded site during that haulout event. Failing these criteria, it was denoted as the first site at which the seal hauled out. For males the main breeding site was that site most frequently recorded consecutively at which the seal was noted as a beachmaster. If the seal was only noted as a bachelor, then it was the most frequently recorded site. Failing this, it was the first site recorded. Pre- and post breeding sites, and additional but less frequented breeding sites were excluded. Total reproductive haulout events: 1 253.

Moult haulout event: The first record of the main moult site was retained as the primary record. The main moult site was either that at which the seal was most frequently recorded consecutively showing physical signs of moult (a portion of the old skin had been lost) or, if moulting was not evident, the most frequently recorded site or, failing these, the first recorded site. Total moult haulout events: 5 356.

Winter haulout event: For the winter haulout, usually one, but up to three separate haulout events were recorded per season for each individual. An elephant seal was assumed to have returned to sea for an extended period if it was not sighted on land for more than 30 days. The primary site retained to represent each winter event was the site at which the seal first hauled out. Total winter haulout events: 4 922.

Examples of basic records for a tagged female and a tagged male seal are given in Appendix 2.

3.3 STATISTICAL ANALYSIS

3.3.1 Tests used

Parametric tests have been developed for dispersal data that fit standard distributions (Reed 1993). All frequency distributions of distances dispersed were, therefore, tested for fit to a number of standard distributions using the X^2 Goodness-of-fit test. These results are listed in Appendix 5. Of importance is the fact that in only two cases were frequency distributions of the data not significantly different from one of the standard distributions. The data were therefore not transformed and non-parametric tests were used to compare the dispersal and dispersion of different categories. These tests have been used in this way in previous studies (Reed 1993, Pärt 1995). The following tests were used:

X^2 Goodness-of-fit Test	For assessing the difference of observed frequency distributions from expected distributions.
Kolmogorov-Smirnov Test	For assessing the difference between the frequency distributions of two independent groups.
Kruskal-Wallis ANOVA	For assessing the difference between the frequency distributions of more than two independent groups.
Wilcoxon Matched Pairs Test	For assessing the differences between the frequency distributions of paired groups.

3.3.2 Samples

Approximately 90 % of females in this dataset reproduced for the first time at the ages of three, four or five years. A few older incipient breeders were recorded, and it is possible that some of these had hauled out to breed elsewhere before, or were the result of the incorrect reading of tags (see Assumptions). In most cases therefore, samples for natal dispersal of females were restricted to those breeding for the first time at ages 3 – 6. Where this was not the case it is noted.

Very few adult elephant seals haul out in the winter (Condy 1979, Kirkman 1999). Those winter haulouts recorded for adults are quite possibly not "true" winter haulouts. Data for the winter haulout were therefore separated into two age groups when the sexes were compared, or when dealing with females alone. These age groups were composed of (1) seals younger than three years (94,9 % of all females and 79,1 % of males), and (2) seals three years and older. When dealing with males alone the two age groups consisted of males younger than six years (97,8 % of males), and those aged six and older.

3.3.3 Sample size

Classes were grouped in an attempt to obtain a minimum sample size of eighty. This was not always possible, especially with male dispersal where the total number of animals recorded hauling out for their first reproductive haulout was 81, and for later reproductive haulouts, 41. Where sample sizes were small (less than 80) this is noted.

3.4 LIMITATIONS AND ASSUMPTIONS

1. Pups were tagged within a week of weaning and are therefore assumed to have been tagged at their natal site. This is considered a reasonable assumption as Panagis (1981) first recorded pups (marked at birth) at sites other than their natal site in mid-November, while pups tagged at weaning (Wilkinson & Bester 1990) moved from their tagging sites starting at the end of October. These dates are at least a month after the first pups would have been weaned, indicating that pups remain at their natal site for the first month after weaning.

2. Tags are assumed to have been read correctly. There are some problematic records in the database, for example, males being recorded on occasion as females with pup. Of more concern are animals that are recorded once after an absence of many years. Obviously aberrant records were excluded from the database. Such records were few, testimony to the high standard of fieldwork done by observers.

3. The search effort is assumed to have remained constant throughout the study, irrespective of the changes in observers, weather or seasons.

4. The age, sex and season are assumed not to influence the behaviour of the seals in such a way that the chance of resighting them would be affected. The topography of the sites is also assumed not to influence the chance of resighting animals.

5. Each haulout event was assumed to be independent. Separate haulouts by one individual were assumed to be unrelated to each other, and were therefore often grouped together in a sample.

6. Characteristics of dispersal were assumed to be unrelated to the number of years that an animal survived. This could result in an age-related bias, as older classes contain only "survivors", and younger age classes, both survivors and animals that had not lived beyond that age class.

7. Age and cohort was assumed to have no effect on dispersal. Except where these were the factors being tested, seals of different ages and cohorts were grouped.

8. It is assumed that movements to other islands, especially Prince Edward Island, have little effect on the patterns shown. This neighbouring island is also a regular haulout site for elephant seals. Seals born on Marion Island have been recorded on Prince Edward Island and it is likely that a number breed, moult and winter at the latter island (Bester 1989). In addition, "missing" haulout events indicate that animals must use other sites, especially for the moult, which is an annual necessity.

9. It is assumed that the sites chosen to represent each haulout event are the sites of importance for those events. This is dealt with more fully in the relevant section above ("Selection of records").

10. Females are assumed to give birth to a pup at each reproductive haulout event, and not merely to haul out for mating. No differentiation between reproductive haulout events is therefore necessary.

3.5 PRESENTATION OF RESULTS

Results are compared by noting the mean distances moved by different groups of seals. In some cases, the percentage of animals recorded hauling out within five, or within one km of the natal site or primary reproductive haulout site is given as a measure of site fidelity. While this merely describes the relative proportions of animals hauling out close to the natal site, the actual resolution used in the statistical analyses is one-tenth of a kilometre.

The graphic displays of results are of two types. Frequency distribution graphs are used in the chapters describing the differences between observed and expected values, between males and females and between types of dispersal and dispersion. Graphs from the chapter dealing with the effects of various factors (Chapter 7) show the mean distances moved (+/- half standard deviation) and the median value. Half standard deviation is used because standard deviations are often very large, obscuring trends, and exceeding the limits of axes. Where necessary frequency distribution graphs are also given for this chapter. Graphs are not displayed for all data. Where the results were very similar for both sexes only one set is shown. Many non-significant results are also not shown.

CHAPTER 4

ARE ELEPHANT SEALS PHILOPATRIC?

4.1 METHODS

4.1.1 Calculation of expected values

To determine whether seals show any fidelity to natal sites, one needs to show that they haul out closer to their natal site than would be expected if their haulouts were random (Caughley 1977, Croxall & Hiby 1982). Expected values were therefore calculated following random walk theory (Caughley 1977). The probabilities of all distances of random displacement from each site, that is, recapture at any distance from any marking site, assuming random movement, were determined using a probability matrix (See Appendix 7 for complete matrix). This matrix took into account two factors:

1. The skewed distribution of elephant seal haulout sites along the coastline of the island (Figure 2.1). These sites are not equidistant from one another and also occur mostly along the northern and eastern coasts of the island. Sites are found at unequal distances from the centre, and the edges of the extended study area. Therefore no two marking sites have the same number of recapture sites within a specific distance. For example, a seal tagged at Blue Petrel Bay can haul out at three sites within a km of its natal site, and a total of 14 within five kilometres (Figure 4.1). A seal tagged at Watertunnel, however, can haul out at only one site

within five kilometres of its natal site (that being its natal site itself). The next haulout site is 5,1 km distant and the next after that one, 6,3 km (Figure 4.1). The greatest concentration (one third) of potential haulout sites for seals tagged at Blue Petrel Bay lie within five kilometres of that site, while the greatest concentration of potential haulout sites for seals tagged at Watertunnel lie between 32 and 42 km away. If seals return at random to any beach on the island, those that are tagged at Blue Petrel Bay are therefore considerably more likely to haul out within five kilometres of their natal site, than those tagged at Watertunnel.

2. Variation in the popularity of sites. Seals showed preference for certain sites, depending on whether they were hauling out to reproduce, to moult or during the winter. Seals returning to the island without regard to previous haulout sites are therefore more likely to haul out at the more popular sites. Figure 4.2 shows the combined effect of popularity and number of sites available, for Blue Petrel Bay and Watertunnel Beach.

These two factors were used to determine the probability of movement between each and every site. From this probability, the probability of movement of each distance in one kilometre interval classes to a maximum possible of 44 kilometres was determined. Since classes were to be of equal size, and a zero km distance was included in the one kilometre class, interval classes are from 0-0,9 km, 1-1,9 km, and so on. The first class was labelled the one kilometre class even though it does not include the distance of one kilometre. Similar labelling applies to all other classes except the 44 km class, which only included distances from 43 to 43,5 km.

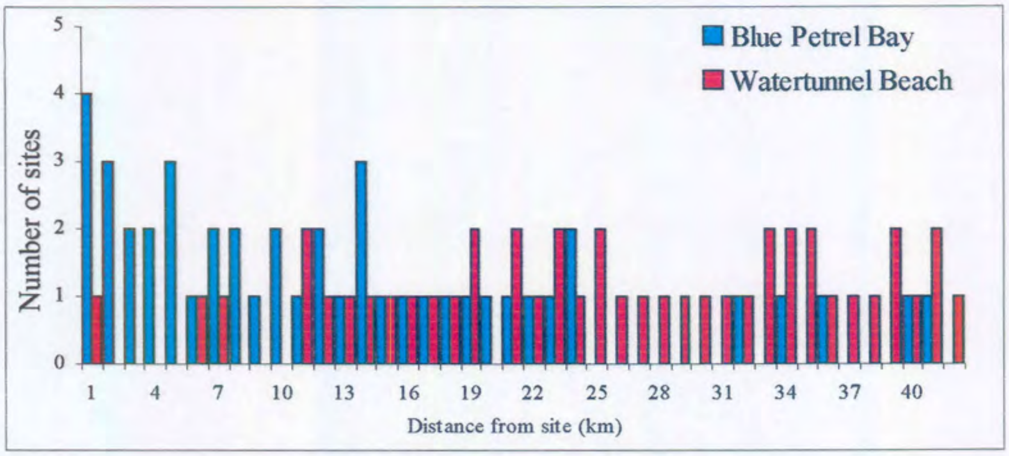

Figure 4.1 Frequency of potential haulout sites, in one-kilometre intervals, from Blue Petrel Bay and Watertunnel Beach.

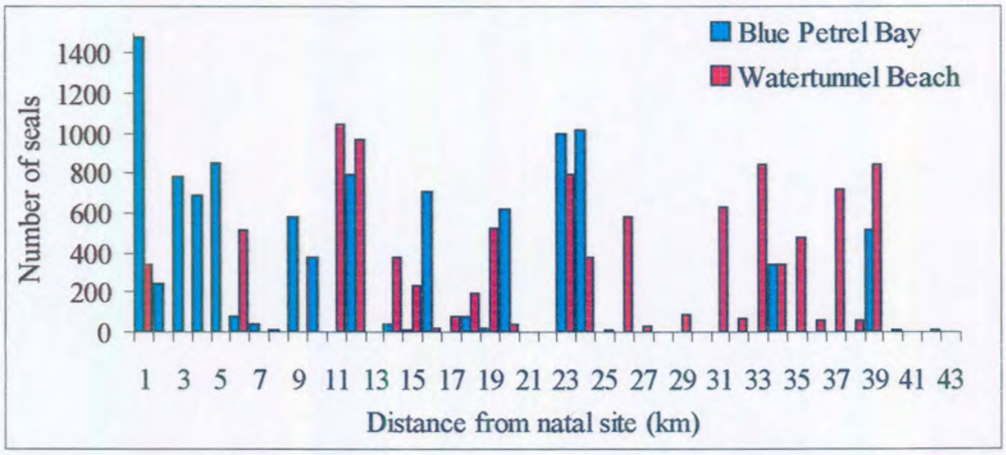

Figure 4.2 Popularity of haulout by breeding southern elephant seals, *Mirounga leonina*, from Marion Island, at sites at one-kilometre intervals distant from Blue Petrel Bay and Watertunnel Beach.

Popularity values of each site for each of the three types of haulouts (breeding, moulting and winter) were determined (Appendix 4). These values were taken as the number of seals, both tagged and untagged, counted at each site during each of these types of haulout, over several years. Breeding site popularity was therefore the number of adult seals counted per site from the 1st of August to the 1st of November over five years (1990 to 1994). Moult popularity was the number of adult seals counted per site from the 1st of December to the 1st of April, and the number of immature seals counted per site from the 1st of November to the 1st of April, over six years (1990 - 1995). Winter haulout popularity was the number of immature seals counted per site from the 1st of April to the 1st of September over four years (1991 - 1994).

The popularity of displacement from each site was determined by summing the popularity values within each one-kilometre interval from that site. The popularity values for each kilometre interval for all sites were then summed. From this a mean probability of displacement for each kilometre interval from natal site, assuming haulout sites were only affected by site popularity, was determined. Figure 4.3 shows these probabilities of displacement.

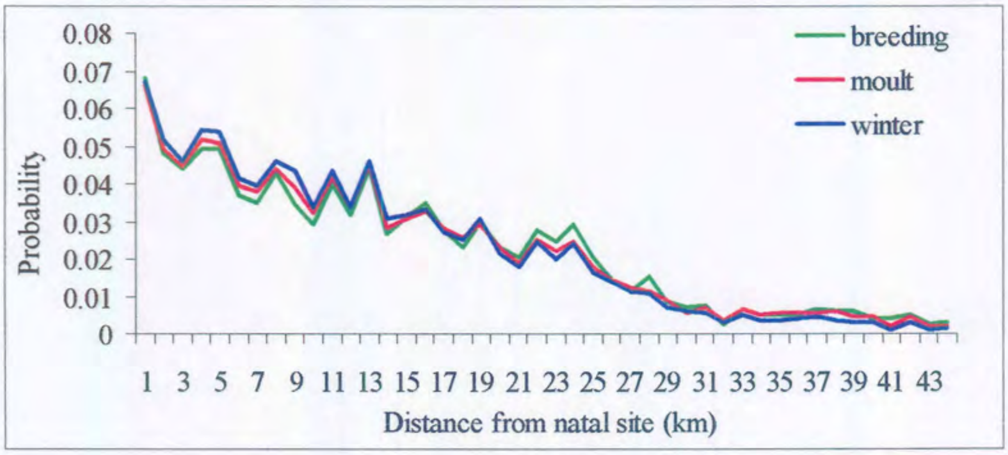

Figure 4.3 Probabilities of displacement from natal site for breeding, moult and winter haulouts, of southern elephant seals, *Mirounga leonina*, at Marion Island.

4.1.2 Samples

The data used were the distances from natal site for all forms of movement, except breeding dispersal, which was the distance from first reproductive haulout site. Tests for all dispersal used data from all reproductive haulouts, while moult dispersion used data from all moult haulouts, and winter dispersion used data for all winter haulouts. Natal dispersal was limited to the data from first reproductive haulouts, and breeding dispersal was limited to all reproductive haulouts except for the first.

4.2 RESULTS

4.2.1 All dispersal

Female southern elephant seals on Marion Island hauled out to breed significantly closer to their natal site than expected (Goodness of Fit Test, $X^2 = 610,9$, d.f. = 43, p = 0,000000). Twenty percent of females bred within one kilometre of their natal site, which was far greater than the 6,8 % expected. More than half (51,4 %) of all reproductive haulouts by females were within five kilometres of the natal site. The expected value here is 25,8 % (Figure 4.4).

Males also showed significant philopatry (Goodness of Fit Test, $X^2 = 140,6$, d.f. = 43, p = 0.000000), even though sample sizes are considerably smaller (n = 123 as opposed to n = 1130). Twenty-two percent of males bred within one kilometre of their natal site, and 62,6 % within five kilometres (Figure 4.5).

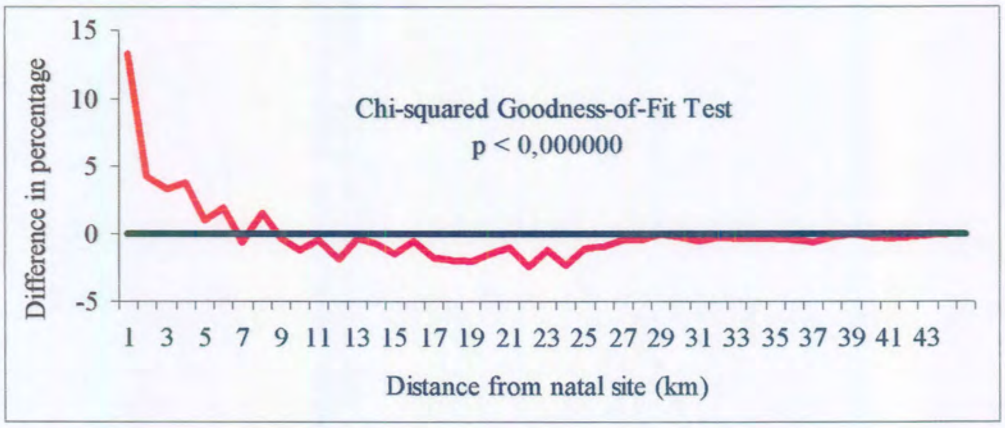

Figure 4.4 Differences between expected and observed percentages of all dispersal of female southern elephant seals, *Mirounga leonina*, at Marion Island. Data are from all reproductive haulout events.

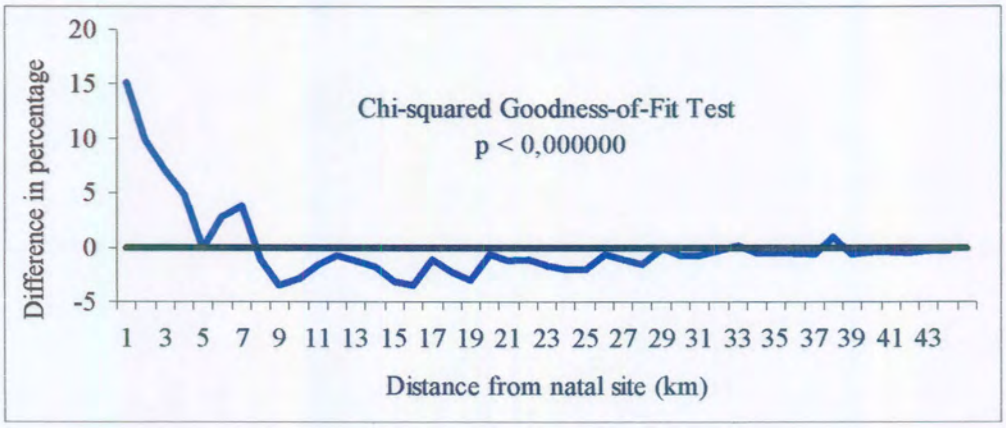

Figure 4.5 Differences between expected and observed percentages of all dispersal of male southern elephant seals, *Mirounga leonina*, at Marion Island. Data are from all reproductive haulout events.

4.2.2 Natal dispersal

Natal dispersal showed similar trends to dispersal for all reproductive haulout events. Females showed significant philopatry (Goodness of Fit Test, $X^2 = 168,1$, d.f. = 43, p = 0,000000) with 17,1 % of females hauling out to breed for the first time within one kilometre of their natal site, and 45,2 % within 5 km of their natal site (Figure 4.6). Again these figures are far higher than the 6,8 % expected within one kilometre, and 25,8 % expected within 5 km.

Of males breeding for the first time, 18,3 % hauled out within a kilometre of their natal site, and 60 % within five kilometres (Figure 4.7). These values are significant (Goodness of Fit Test, $X^2 = 71,2$, d.f. = 43, p = 0,0044).

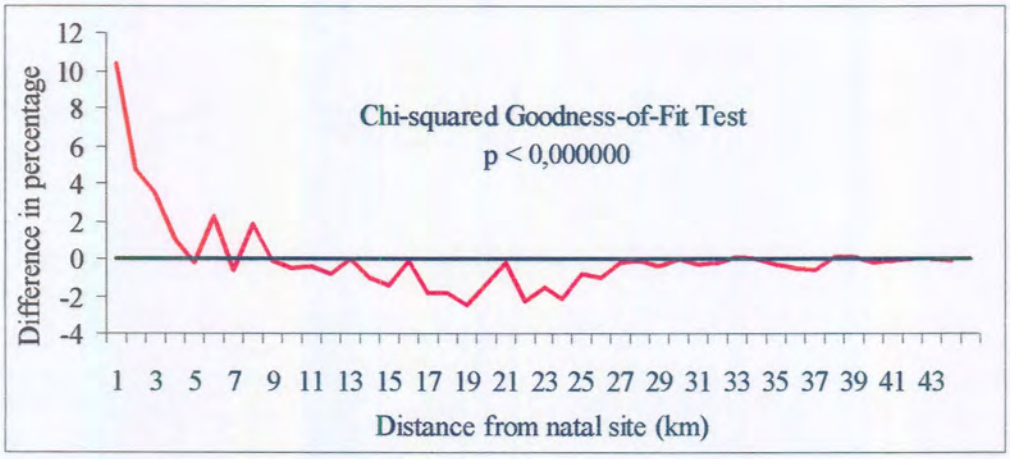

Figure 4.6 Differences between expected and observed percentages of natal dispersal of female southern elephant seals, *Mirounga leonina*, at Marion Island. Data are from first reproductive haulouts only.

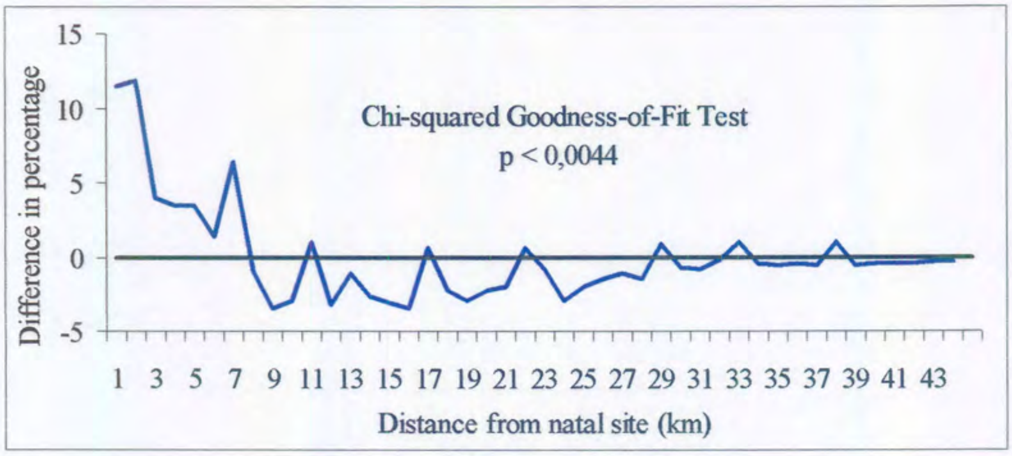

Figure 4.7 Differences between expected and observed percentages of natal dispersal of male southern elephant seals, *Mirounga leonina*, at Marion Island. Data are from first reproductive haulouts only.

4.2.3 Breeding dispersal

Female elephant seals returned significantly closer to their first reproductive haulout site than would be expected by chance alone (Goodness of Fit Test, n = 541, X^2 = 549,05, d.f. = 43, p = 0,000000). Whereas 6,8 % of females were expected to haul out within a kilometre of their first reproductive site, 26,4 % actually did (Figure 4.8). Over half of females (61,4 %) reproduced within five kilometres of their first reproductive site. This was more than double the 25,8 % expected.

Males also hauled out significantly closer to their first reproductive site when returning to reproduce in later years, than was expected by chance (Goodness of Fit Test, n = 41, X^2 = 99,0, d.f. = 43, p = 0,000003). A total of 31,7 % of males returned to within 1 km of their first reproductive haulout site, and almost nine tenths (87,8 %) to within five kilometres, which is far higher than the 6,8 % and 25,8 % expected (Figure 4.9).

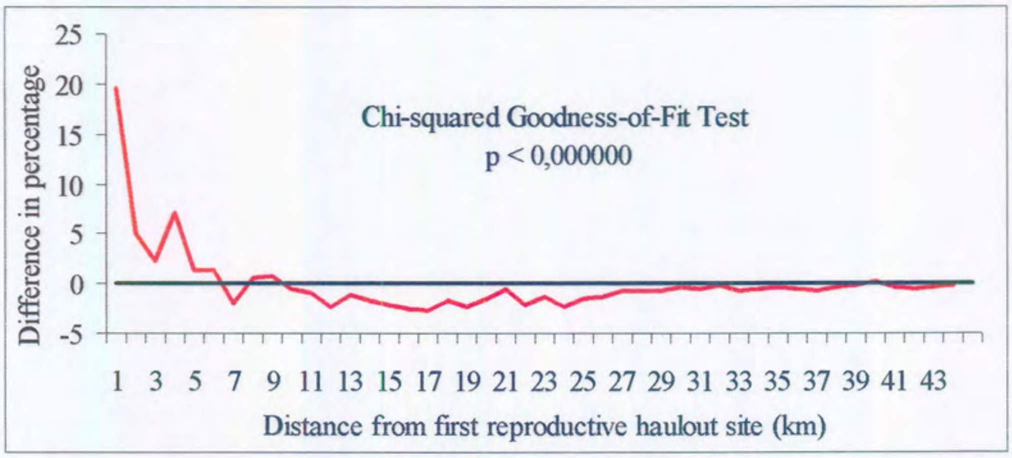

Figure 4.8 Differences between expected and observed percentages of breeding dispersal of female southern elephant seals, *Mirounga leonina*, at Marion Island. Data are from all reproductive haulouts except the first.

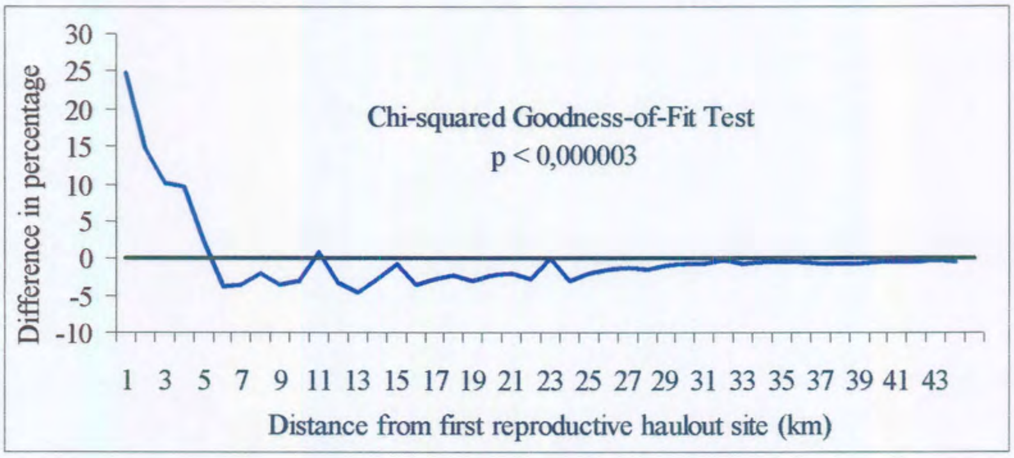

Figure 4.9 Differences between expected and observed percentages of breeding dispersal of male southern elephant seals, *Mirounga leonina*, at Marion Island. Data are from all reproductive haulouts except the first.

4.2.4 Moult dispersion

Female southern elephant seals at Marion Island moulted significantly closer to their natal site than would be expected of a random return to Marion Island (X^2 Goodness-of-fit Test, $n = 2916$, $X^2 = 513$, d.f. $= 43$, $p < 0,000000$). Eleven percent hauled out within 1 km of their natal site to moult. This was almost twice the expected 6,6 %. In addition 39,7 % hauled out within 5 km of their natal site, some 15 % more than the expected 26,3% (Figure 4.10).

As with females, male seals hauled out significantly closer to their natal sites than was expected (Goodness-of-fit Test, $n = 2412$, $X^2 = 546$, d.f. $= 43$, $p < 0,000000$). A total of 12,8 %, which was almost double the expected 6,6 %, hauled out within one kilometre of their natal site. Further, 42,2 % hauled out within five kilometres of the natal site, far greater than the expected 26,3 % (Figure 4.11).

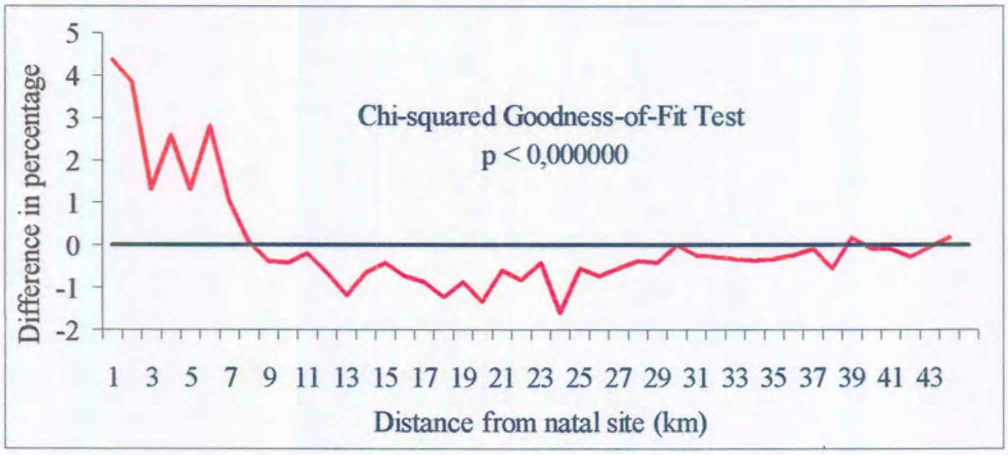

Figure 4.10 Differences between expected and observed percentages of moult dispersion of female southern elephant seals, *Mirounga leonina*, at Marion Island.

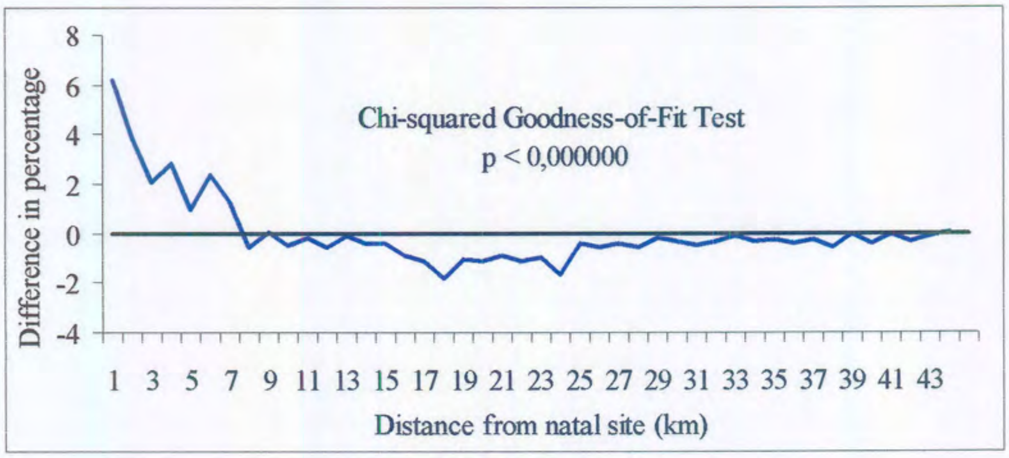

Figure 4.11 Differences between expected and observed percentages of moult dispersion of male southern elephant seals, *Mirounga leonina*, at Marion Island.

4.2.5 Winter dispersion

Female elephant seals hauled out to winter significantly closer to their natal site than was expected (Goodness-of-Fit Test, $X^2 = 223$, d.f. = 43, $p < 0{,}000000$). The proportion of females hauling out within a kilometre of their natal site was 9,6%, which was approximately 50 % more than the expected 6,7 %. More than a third (36,4 %) of females hauled out to winter within five kilometres of their natal site, compared to the expected 27,3 % (Figure 4.12).

A highly significant result was also found for male winter dispersion (Goodness-of-Fit Test, $X^2 = 520{,}36$, d.f. = 43, $p < 0{,}000000$). Almost twice as many (11,7 %) males hauled out within a kilometre of their natal site than the expected 6,7 %. Forty-two percent of males hauled out to winter within five kilometres of their natal site, compared to the expected 27,3 % (Figure 4.13).

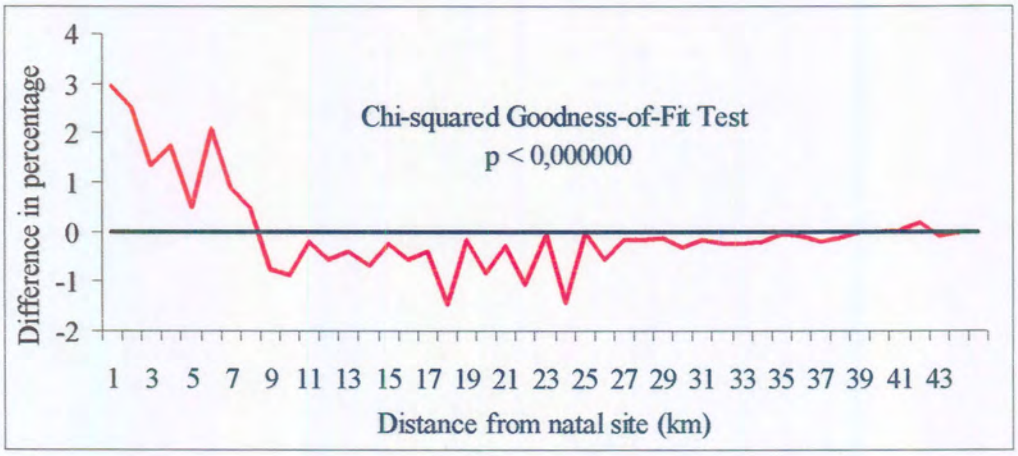

Figure 4.12 Differences between expected and observed percentages of winter dispersion of female southern elephant seals, *Mirounga leonina*, at Marion Island.

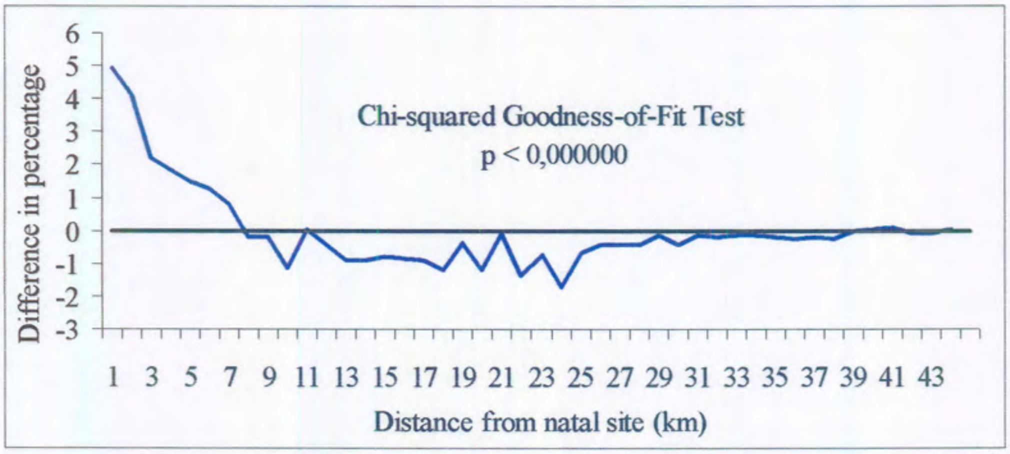

Figure 4.13 Differences between expected and observed percentages of winter dispersion of male southern elephant seals, *Mirounga leonina*, at Marion Island.

4.3 DISCUSSION

4.3.1 Methods

Types of data used

Few studies of pinnipeds have dispersal or dispersion as their major aim. In most, information related to these movements is merely presented as a conjunct of a larger study, or reported anecdotally. The study of dispersal and dispersion in pinnipeds is not easy. While a large data set of sightings of marked animals is required, the observation of marine animals is difficult, especially as their haulout sites are often very isolated and in environments hostile to the observers. Studies are also often limited to sightings from only one or two of many potential haulout sites. Such studies rely solely on the percentage of tagged animals returning to their site of marking, and therefore on a fidelity index (Lunn & Boyd 1991, Baker *et al.* 1995, Croxall & Hiby 1983). This does not, however, consider patterns of distance dispersed from site of origin.

A number of studies have noted the distance from site of origin to subsequent sites and have therefore considered the frequency distribution of dispersal and dispersion distances (Lenglart & Bester 1982, Wilkinson & Bester 1990, Lunn & Boyd 1991, Pomeroy *et al.* 1994, Thompson *et al.* 1994). This is also the approach used in this study. The statistical analysis of such data can assess more than just the difference between two means or two percentages, but also the difference in the shapes of frequency distributions (StatSoft 1994). This allows one to consider patterns of dispersal, and not just site fidelity.

Determining expected values

Previous studies of dispersal involving large numbers of marked individuals, especially of fish, have generally been based on single-release-site multiple-recapture-site models. Recaptures are either along a single dimension, for example where individuals are resighted along a coastline (Attwood & Bennett 1994), or from two-dimensional plane where individuals were resighted over an area (Hilborn 1989, 1990, Anganuzzi *et al.* 1994). Random probabilities of displacement to recapture sites are determined by a series of mathematical functions (Reviewed in Hilborn 1990).

This study, however, involved, not only multiple recapture sites, but also multiple marking sites. Elephant seals were tagged at 41, and resighted at 54 different sites. Previous studies using a multiple-marking-site multiple-recapture-site format could not be identified. Fortunately both marking and recapture in this study took place along only a single dimension, this being the coastline of Marion Island. While mathematical functions were not developed for this thesis, they will be in a future study.

4.3.2 Dispersal

The results of this study demonstrate that southern elephant seals show a high degree of fidelity to their natal site, and to the site of first reproduction. This is not unusual and has been shown for many species (reviewed in Greenwood 1980 and Dobson 1982). A number of species of pinnipeds are also highly philopatric (reviewed in Chapter 1). This is to be expected of animals that migrate long distances to foraging sites within a vast habitat with few apparent barriers to movement, and yet in which suitable breeding sites are few and isolated (Bartholomew 1970). Where pinnipeds breed at ephemeral and unstable sites, far less site fidelity is shown. Weddell seals haul out to reproduce on sea-ice, which is highly variable both spatially and temporally, and therefore exhibit lower levels of fidelity compared to seals breeding on land (Croxall & Hiby 1983). Other species of marine animals with similar life history characteristics to those of southern elephant seals also show similar site fidelity. These animals include species of whales (Salden *et al.* 1999), turtles (Meylan *et al.* 1990) and seabirds (Osorio-Beristain & Drummond 1993). Further discussion of the possible reasons for breeding site fidelity is found in Chapter 6, and in the conclusion.

4.3.3 Dispersion

A number of species of birds show fidelity to sites used for reasons other than reproduction. This includes fidelity to moult site by many species of migratory waterfowl (Anderson & Sterling 1974, Williams 1979, Szymczak &Rexstad 1991, Bowman & Brown 1992, Bollinger & Derksen 1996, Flint *et al.* 2000), and fidelity to winter site by various other species of migratory birds (Schroeder & Braun 1993, Hertzog & Keppie 1980, Schroeder 1985, 1988, Wilson *et al.* 1991, Warren *et al.* 1992, Raveling 1979). Flint *et al.* (2000) stated that it is likely that fidelity to moult or winter sites results from reasons other than those of advantage in breeding site fidelity. Prior knowledge of the location of patchily distributed and isolated resources may be of advantage (Warren *et al.* 1992).

Elephant seals also return to isolated sites in a large area with a limited number of good sites. There is, however, one important difference. Elephant seals undertake an annual double migration (Bester & Pansegrouw 1992, De Long *et al.* 1992, Stewart & De Long

1995, Jonker & Bester 1998), and therefore generally return to their natal island to moult and to winter. Migratory birds move away from their natal site to separate and distant moult and winter sites. While some elephant seals use islands close to foraging areas for the moult (Tierney 1977, Bester 1988, Lewis *et al.* 1996) most do not, even where they are available, and prefer to return to their natal island. It is possible that the temporal discontinuity between birth and first reproduction could lead to a loss of familiarity with the natal site in migratory species (Morton 1992, Pärt 1995). Returning as an immature may help maintain familiarity with the natal site (Pärt 1991). Further investigation of this hypothesis would require the assessment of the effect of prior haulout sites on the location of subsequent reproductive sites.

Moult

The fidelity to natal site shown by moulting southern elephant seals on Marion Island is different to the behaviour of the Macquarie Island population (Nichols 1970). It was suggested by Nichols (1970) that the dispersion of moulting seals away from natal sites on the latter island was likely due to the absence of sites with moult wallows in the natal area of the marked seals. On Marion Island, however, moult wallows are associated with most breeding beaches (Panagis 1984). Seals from Marion Island, therefore, do not need to move far from their natal site to find suitable moult sites. To understand the importance of the influence of the local terrestrial environment on the choice of moult site, further research will be needed to compare the characteristics of dispersal of different populations of southern elephant seals in relation to topographic features.

Winter

Nichols (1970) found a significant concentration of marked seals, from Macquarie Island, hauling out for the winter at their natal site. Elephant seals on Marion Island also winter closer to their natal site than is expected. Although the exact requirements for a winter haulout site are not known, it appears that they are nothing more than a beach on which to rest. Any accessible beach should therefore be suitable. It may be that maintaining familiarity with the natal site, or the area of the natal site, as suggested for the moult, is also of importance in explaining winter haulout site fidelity.

CHAPTER 5

COMPARING DISPERSAL AND DISPERSION

5.1 METHODS

5.1.1 Dispersal

Natal dispersal and breeding dispersal

All data for reproductive haulouts were used. Breeding dispersal distances were taken from the primary reproductive haulout site. For males the sample size for natal dispersal was 81, and only 41 for breeding dispersal.

Dispersal distance to later reproductive haulout sites from the natal site and from the first reproductive haulout site

The distances from natal site and from primary reproductive haulout site were compared using paired samples. The sample size for males was only 41.

5.1.2 Dispersion

Three comparisons were made between moult and winter dispersion for each sex. The first compared all data. The second compared the data of immature animals. For females this excluded animals older than two years of age (mostly adults and only approximately five percent of the total). For males all animals older than five years were excluded. The third comparison included data for all seals older than two years, for females, and all animals older than five years for males. Sample sizes were small only for the adult comparisons. While adult females were recorded hauling out to moult on 1280 occasions, they were only recorded hauling out to winter on 100 occasions. Adult males were recorded moulting 152 times, and during the winter, only 53 times.

5.1.3 Dispersal and dispersion

All dispersal and moult dispersion

Two comparisons were made for each sex. The first compared the distance from natal site for all moult dispersion to the distance from natal site for all reproductive haulout events. The second restricted age to animals older than two years for females, and older than five years for males.

All dispersal and winter dispersion

Two comparisons were made for each sex, following the age classes noted above. The sample for females hauling out to winter as adults included only 100 individual haulouts, while the sample for males included only 53 individual haulouts.

5.2 RESULTS

5.2.1 Dispersal

Natal dispersal and breeding dispersal

Breeding dispersal is significantly less than natal dispersal for female elephant seals (Kolmogorov-Smirnov, p < 0,001). Females were displaced a shorter distance from their site of first reproduction when returning to reproduce in subsequent years (x = 6,1 km), than they were displaced between their birth site and their primary haulout site (x = 8,6 km). Moreover, only 46,3 % of first time breeders hauled out within a kilometre of their natal site, while 61,4 % of returning breeders hauled out within the same distance of their primary reproductive haulout site (Figure 5.1).

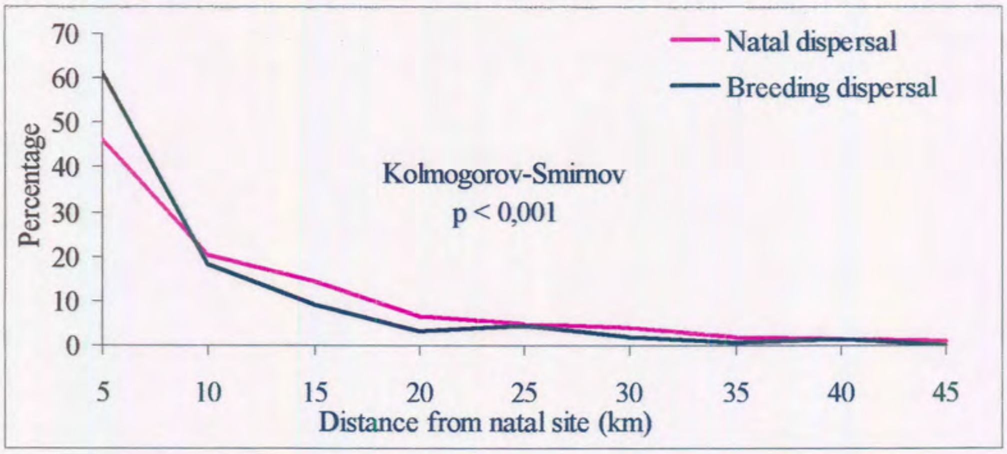

Figure 5.1 Percentage distributions of natal and breeding dispersal haulouts of female southern elephant seals, *Mirounga leonina*, at Marion Island. Percentage natal dispersal is shown in five kilometre intervals from the natal site, while percentage breeding dispersal is shown in five kilometre intervals from the first reproductive haulout site.

Males also showed significantly less breeding dispersal than natal dispersal (Kolmogorov-Smirnov, $p < 0,05$). The distance males dispersed from their site of first reproduction to subsequent reproductive haulouts ($x = 3,1$ km) was approximately half the distance from natal site to the site of first reproduction ($x = 6,4$ km). Although a considerable percentage of male seals bred within five kilometres of their natal site (61,0 %) this is much less than the 87,8 % of males returning to breed again within five kilometres of their first reproductive site (Figure 5.2).

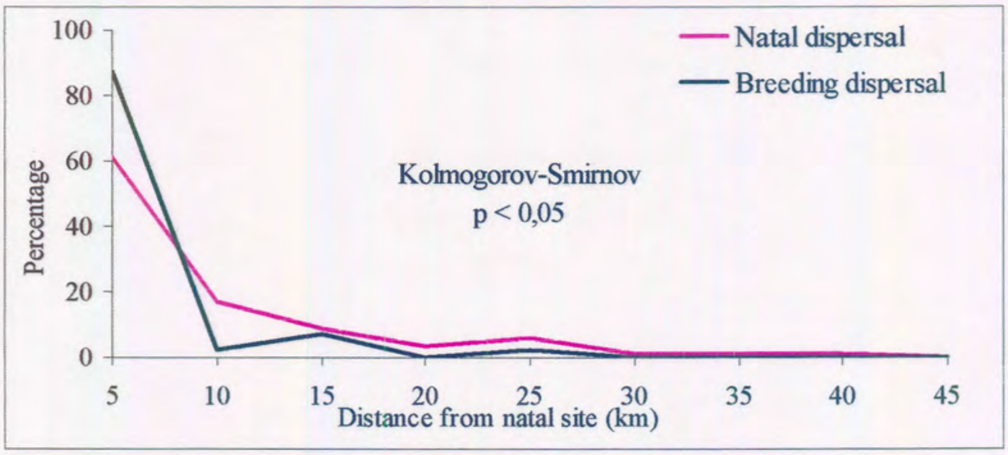

Figure 5.2 Percentage distributions of natal and breeding dispersal haulouts of male southern elephant seals, *Mirounga leonina*, at Marion Island. Percentage natal dispersal is shown in five kilometre intervals from the natal site, while percentage breeding dispersal is shown in five kilometre intervals from the first reproductive haulout site.

Dispersal distance to later reproductive haulout sites from the natal site and from the first reproductive haulout site

Neither female (Wilcoxon Matched Pairs Test, n = 541, t = 44599, z = 1,3, p = 0,19) nor male (Wilcoxon Matched Pairs Test, n = 41, t = 238,5, z = 1,5, p = 0,14) seals returning to breed, subsequent to their first reproductive haulout, showed any significant difference between the distances displaced from their natal site and from their site of first reproduction (Figure 5.3).

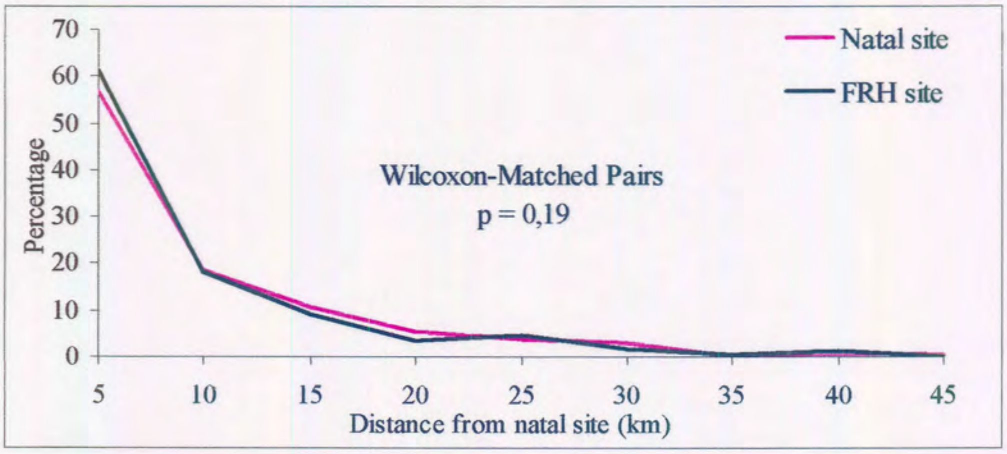

Figure 5.3 Percentage distributions of reproductive haulout events subsequent to the first for female southern elephant seals, *Mirounga leonina*, at Marion Island. Percentage dispersal is shown in five kilometre intervals from the natal site and the site of first reproduction (FRH site).

5.2.2 Dispersion

A significant difference was found between moult and winter dispersion of females when the data from all age classes was used (Kolmogorov-Smirnov, p < 0,001), however when comparing only immature females (younger than three years of age) no significant difference was found (Kolmogorov-Smirnov, p > 0,05). When females hauled out for the moult they dispersed a mean distance of 10,2 km, which is almost exactly the same as the 10,1 km dispersed to winter sites (Figure 5.4). While there was a much greater difference in dispersion when comparing adult females (older than two years), again no significance was shown (Kolmogorov-Smirnov, p >0,05). The mean distance dispersed by moulting adult females was 8,6 km, and to winter haulouts by adult females was 10,6 km.

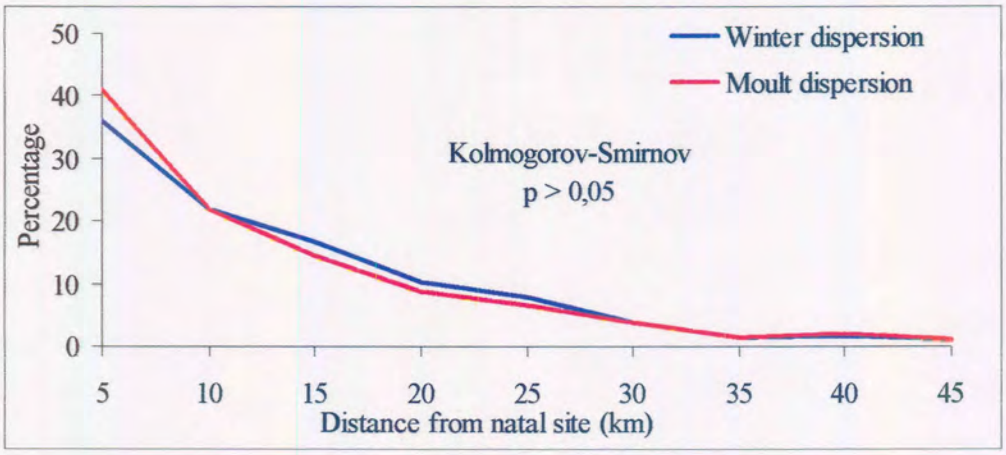

Figure 5.4 Percentage distributions of moult and winter dispersal haulouts of immature (less than three years of age) female southern elephant seals, *Mirounga leonina*, at Marion Island. Percentage dispersion is shown in five kilometre intervals from the natal site.

No significant difference existed between moult dispersion and winter dispersion for male elephant seals, whether all age classes were compared together or when adults and immatures were compared separately (Kolmogorov-Smirnov, p > 0,05 in all cases).

5.2.3 Dispersal and dispersion

All dispersal and moult dispersion

Female elephant seals hauled out significantly closer to their natal site to breed than to moult (Kolmogorov-Smirnov, $p < 0,001$). The mean distance from natal site to reproductive site was 7,8 km, while that to moult site was 9,6 km. While 51,3 % of females bred within five kilometres of their natal site, only 40,9 % moulted within this distance (Figure 5.5). Seals older than the age of two showed the same pattern (Kolmogorov-Smirnov, $p < 0,001$). The mean distance displaced from natal site by adult moulters was 8,6 km, while the mean distance displaced to reproductive sites was 7,8 km.

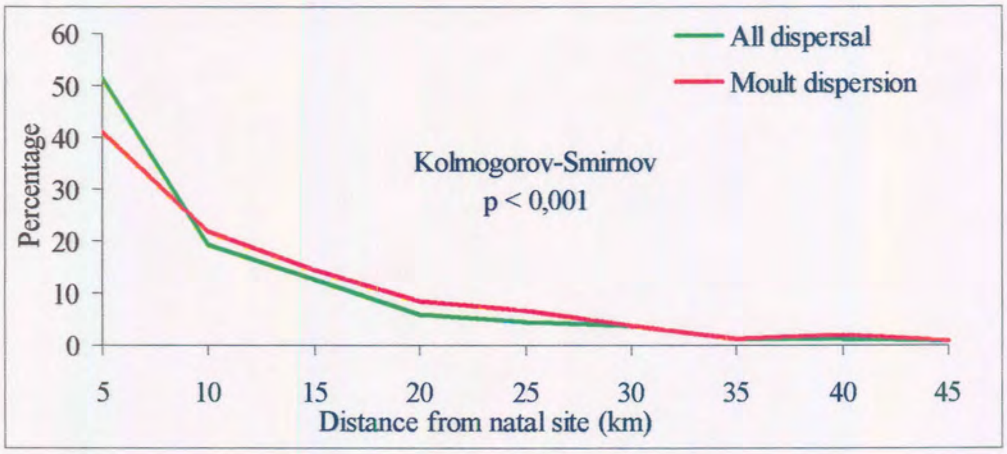

Figure 5.5 Percentage distributions of dispersal and moult dispersion haulouts of female southern elephant seals, *Mirounga leonina*, at Marion Island. Percentage dispersal and dispersion distances are shown in five kilometre intervals from the natal site.

Male seals also returned significantly closer to their natal site when hauling out to breed than for the moult (Kolmogorov-Smirnov, $p < 0,001$). The mean distance between breeding site and natal site was six kilometres, considerably less than that between moult site and natal site (x = 9,0 km). Some 62,6 % of male seals hauled out to breed within five kilometres of their natal site compared to the 42,3 % that hauled out to moult within this distance. Adult males considered alone did not show any significant difference between dispersal and moult dispersion (Kolmogorov-Smirnov, $p > 0,05$).

All dispersal and winter dispersion

As with the moult, female seals that hauled out to winter did not return as close to their natal site as they did when hauling out during the breeding season (Kolmogorov-Smirnov, $p < 0,001$). The mean distance displaced to breeding site was only 7,8 km, while that to winter site was 10,1 km. The percentage of seals hauling out within five kilometres of their natal site to winter was just more than a third (36,0 %), considerably less than the 51,3 % breeding within this distance (Figure 5.6). A significant difference

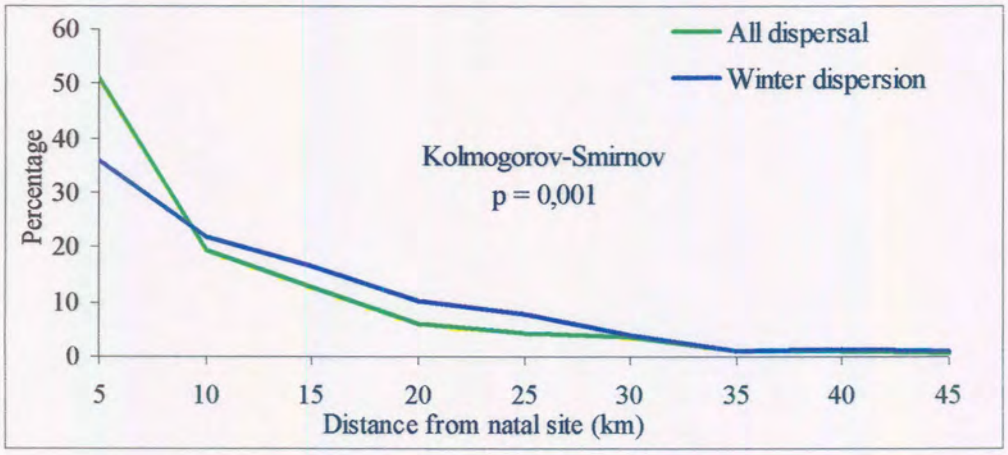

Figure 5.6 Percentage distributions of dispersal and winter dispersion haulouts of female southern elephant seals, *Mirounga leonina*, at Marion Island. Percentage dispersal and dispersion distances are shown in five kilometre intervals from the natal site.

was also shown for seals older than the age of two (Kolmogorov-Smirnov, p < 0,001). The mean distance for the winter dispersion of adult females was 10,6 km, compared to the mean for all dispersal of 7,8 km.

The mean distance that male seals were displaced from natal site to winter site (x = 9,3 km) was significantly less than the six km to breeding site (Kolmogorov-Smirnov, p < 0,001). The percentage of male seals hauling out to winter within five kilometres of their natal site is identical to that hauling out in the same area to moult (42,3 %), and again much less than the 62,6 % for the breeding season. No significant difference exists between dispersal and moult dispersion of adult males (Kolmogorov-Smirnov, p > 0,05).

5.3 DISCUSSION

5.3.1 Dispersal

Southern elephant seals at Marion Island show less breeding dispersal than natal dispersal. They move much further from their natal site to breed for the first time, than they move from their site of first reproduction to sites of subsequent reproduction. Similar patterns of behaviour are described for most species of mammals and birds (reviewed in Greenwood 1980, Dobson 1982), including a number of species of seals. While female Weddell seals seldom return to breed at sites at which they were tagged as pups, they breed close to their own previous reproductive haulout sites (Stirling 1969, Croxall & Hiby 1983).

Theoretically, several reasons may result in greater natal dispersal compared to breeding dispersal, including the following.

1. Once an animal has dispersed to its site of first reproduction, it may have already avoided the negative effects consequent upon breeding at its natal site (see Chapter 1). There is therefore little need for further dispersal, and low breeding dispersal should result. A further line of evidence supporting this hypothesis is the lack of an effect of age on breeding dispersal of elephant seals at Marion Island (see Chapter 7). It may be that elephant seals are navigating as accurately as possible when returning to their first breeding site during subsequent reproductive haulouts events.

2. The greater length of time between weaning and the first reproductive haulout compared to the length of time between consecutive reproductive haulouts may result in less familiarity with the natal site compared to the site of first reproduction (Morton 1992). In Chapter 7 it is shown that age at first reproduction has a significant effect on natal dispersal, with older first time breeders dispersing further than younger ones, which may also indicate that familiarity with a site decreases with the length of absence from that site.

5.3.2 Dispersion

There is no difference between moult dispersion and winter dispersion for elephant seals at Marion Island, in contrast to the pattern found by Nichols (1970) for elephant seals at Macquarie Island. He indicated that, while wintering seals hauled out close to their natal site, moulting seals did not, and explained this as being due to the location of moult wallows. On Marion Island moult wallows are found adjacent to most beaches and seals need not move far, if at all, from their natal site to a moult wallow.

There is, however, reason to believe that elephant seals should show less site fidelity during the moult haulout than during the winter haulout, since seals are less able to move between sites during the moult, and are therefore less able to move towards a specific site. The seals mobility is reduced by their reluctance to enter the water while moulting, due to the condition of their skin (pers, obs.), and also, possibly, due to the presence of killer whales, *Orcinus orca*, in the waters around the island during the summer (Condy *et al.* 1978). Unfortunately the analysis of the data will be unable to detect a difference due to reduced movement between site, because of the difference between the methods used to select the record taken to represent each haulout event, for the moult and the winter haulouts. While the representative record for a moult haulout event was chosen from records of the site at which an animal was recorded to spend its time actually moulting, the winter haulout representative record was selected as the record of the first site used during a haulout event, in lieu of an identifiable major haulout site.

5.3.3 Dispersal and dispersion

Elephant seals haul out far closer to their natal site during the breeding season than during the moult or winter. Other studies of pinnipeds have indicated that the greater fidelity to natal site of the breeding season may be a common pattern. Huber *et al.* (1991) showed that while most female northern elephant seals bred on their natal island, and that there was little movement between breeding sites, it was common for females to breed on one island and to moult on another. Nichols (1970) also found that southern elephant seals at Macquarie Island did not haul out as close to their natal site for the winter, as they did for the breeding season, while adult female Weddell seals recorded with a pup during the breeding season showed far greater fidelity to previous pupping sites than adult females without pups (Stirling 1969).

There are a number of possible explanations for lesser site fidelity during dispersion compared to dispersal, including the following.

1. Returning to the natal site for the moult or winter is of less importance than for the breeding season as dispersion haulouts are not directly linked to reproductive success. Pärt (1995) stated that the accuracy of return to a site was a balance between the costs of time spent in finding that site, and the benefits from use of that site. It follows that where the quality of site is not as important, as postulated for moult and winter haulouts, it is not worth investing much time in finding the natal site.

2. Immature seals hauling out for the moult or winter are unable to compete successfully with adults at breeding colonies. Stirling (1969) stated that this may be the reason that immature Weddell seals disperse further than adults.

3. Seals hauling out for the moult or winter are actively seeking sites with characteristics that are not found at popular breeding sites. It was postulated by Bester & Van Niekerk (1984) that elephant seals at the Iles Kerguelen selected moult sites that had suitable moult wallows, a requirement that would not be needed for a breeding site, and therefore not necessarily found at the natal site. This hypothesis may be valid for the moult haulout, but is difficult to apply to the winter haulout.

These hypotheses are all discussed further in Chapter 7, the first two in the section dealing with the effects of age, and the last, in the section dealing with the effects of disturbance and pre-weaning mortality.

CHAPTER 6

SEX BIAS IN DISPERSAL AND DISPERSION

6.1 METHODS

No haulout events were excluded in testing for sex-related differences for each type of dispersal and dispersion. A supplementary analysis was necessary in the case of winter dispersion to compensate for an age-related bias. While males hauled out to winter up to the age of six years, very few females (about five percent of the total) hauled out for the winter beyond the age of two years. Therefore an independent comparison of males and females younger than three years of age was made.

The sample size for male breeding dispersal included only 41 haulout events, and that for male natal dispersal, only 81 haulout events. All other groups had sample sizes of greater than 120. Distributions were compared using the Kolmogorov-Smirnov Test.

6.2 RESULTS

6.2.1 All dispersal

Females dispersed significantly further from their natal site than males (Kolmogorov-Smirnov $p < 0,01$). Females bred an average of 7,8 kilometres from their natal site, 1,8 kilometres further than males. Approximately two-thirds (62,6 %) of males bred within five kilometres of their natal site compared to only half (51,3 %) of females (Figure 6.1).

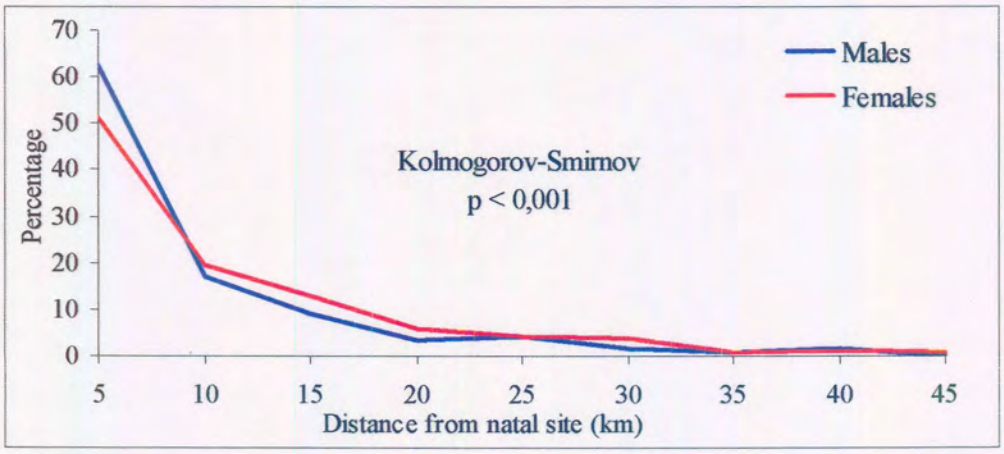

Figure 6.1 Percentages of female and male southern elephant seals, *Mirounga leonina*, at Marion Island hauling out in five kilometre intervals from their natal site for all reproductive haul-outs.

6.2.2 Natal dispersal

The pattern is similar when natal dispersal alone is considered (Kolmogorov-Smirnov $p < 0{,}01$), with 61 % of males having bred for the first time within five kilometres of their natal site, compared to 46,3 % of females (Figure 6.2). Females were displaced a mean distance of 8,6 km from their natal site, significantly further than the 6,4 km of males.

6.2.3 Breeding dispersal

Female elephant seals showed significantly greater breeding dispersal than males (Kolmogorov-Smirnov $p < 0{,}01$). Whereas only 61 % of females returned to breed within five kilometres of their natal site, 88 % of males do. Males hauled out an average of 3,1 km from the first reproductive haulout site, approximately half the 6,1 km of females.

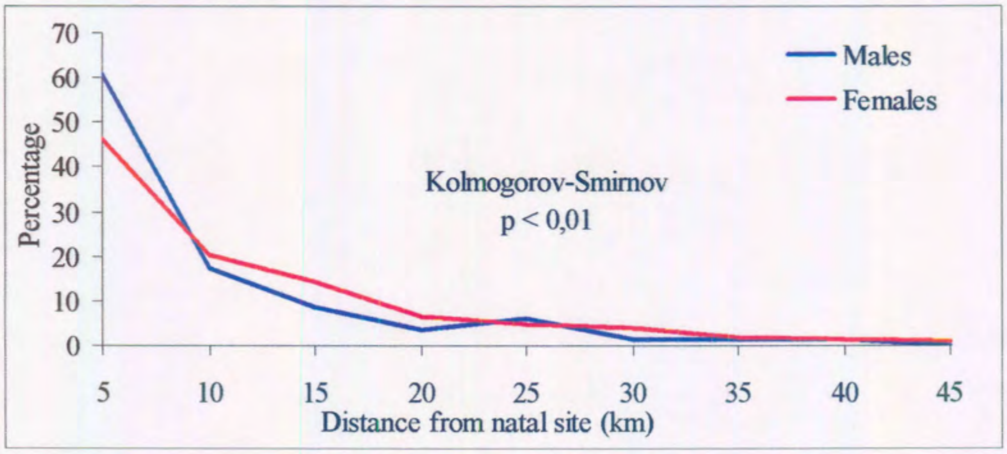

Figure 6.2 Percentages of female and male southern elephant seals, *Mirounga leonina*, at Marion Island hauling out in five kilometre intervals from their natal site for their first reproductive haulouts.

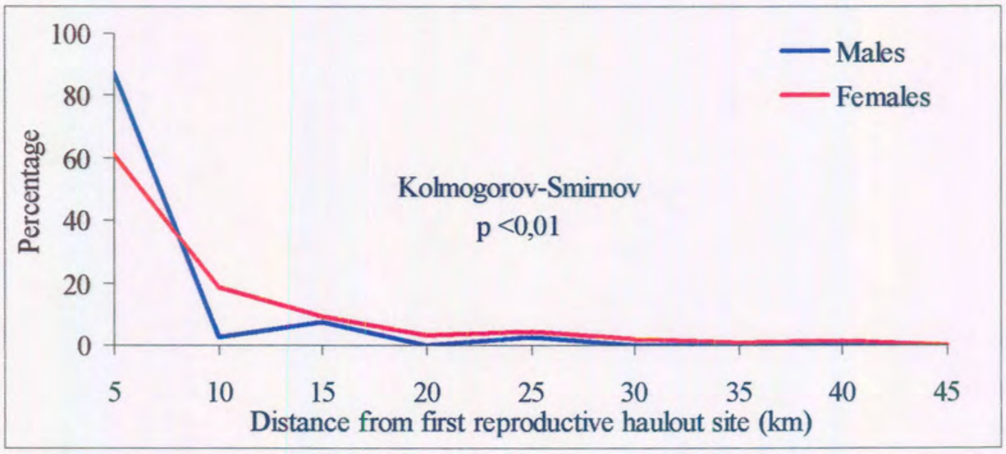

Figure 6.3 Percentages of female and male southern elephant seals, *Mirounga leonina*, at Marion Island hauling out in five kilometre intervals from their first reproductive haulout site, on subsequent reproductive haulouts.

6.2.4 Moult dispersion

No significant sex bias was evident for moult dispersion (Kolmogorov-Smirnov p > 0,05). This is reflected in the very small difference between the 11 % of females, and the 12,6 % of males that hauled out within a kilometre of their natal site (Figure 6.4). Female seals moulted an average of 9,5 km from their natal site, only 0,5 km further than that of males.

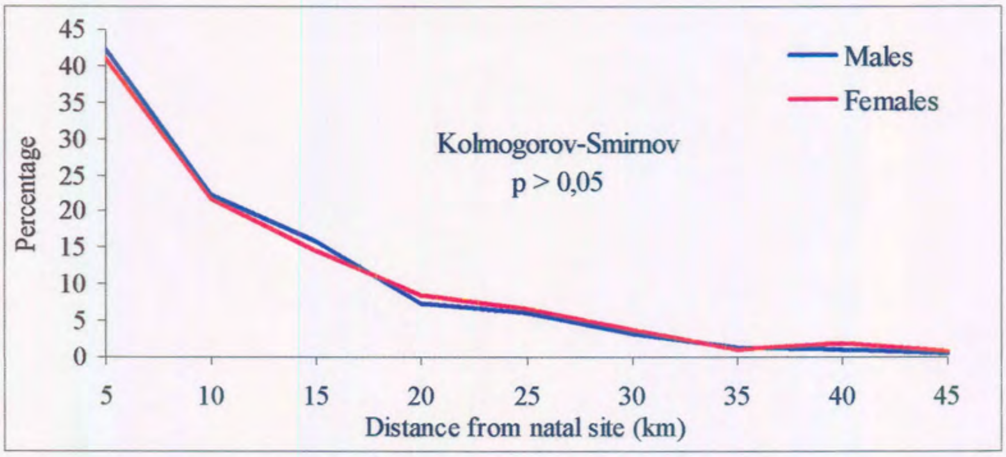

Figure 6.4 Percentages of female and male southern elephant seals, *Mirounga leonina*, at Marion Island hauling out in five kilometre intervals from their natal site for all moult haulouts.

6.2.5 Winter dispersion

Females were recorded significantly further from their natal site during the winter haulout than were males, when all ages are included (Kolmogorov-Smirnov p < 0,01). The percentage of females hauling out within five kilometres of their natal site was 36 %, compared to 42,3 % of males. The mean distance displaced by females was 10,2 km, and by males it was 9,3 km. When all animals older than two years of age were excluded, a different picture emerged, with no difference apparent between the sexes for winter dispersion (Kolmogorov-Smirnov p > 0,05). Females of younger than three years of age moved a mean distance of 10,4 km from their natal site, and males, 10,3 km. The percentage of females hauling out within one kilometre of their natal site (9,6 %) was only slightly less than the 11 % of males (Figure 6.5).

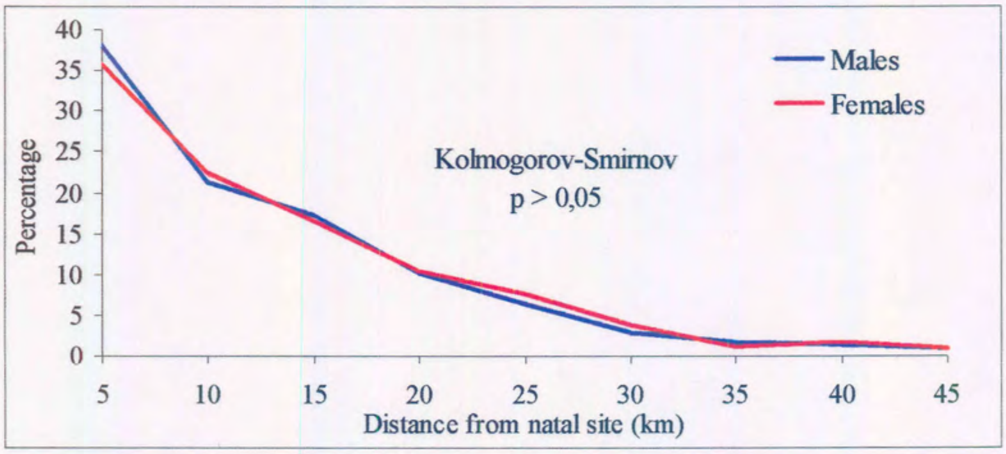

Figure 6.5 Percentages of female and male southern elephant seals, *Mirounga leonina*, at Marion Island hauling out in five kilometre intervals from their natal site for all winter haulouts.

6.3 DISCUSSION

6.3.1 Dispersal

A comparison with dispersal in other species and populations of pinnipeds

Previous studies of pinnipeds have indicated that dispersal is male biased (Carrick & Ingham 1962b, Nichols 1970, Kaufman 1975 in Greenwood 1980, Warnecke 1975 in Dobson 1982, Baker *et al.* 1995). The only other study of southern elephant seals, comparing the dispersal of males and females, found greater philopatry for females of the population at Macquarie Island (Nichols 1970). In contrast this study finds that females disperse further than males. It is possible that the difference between this and the Macquarie Island study result from differences in techniques employed. The earlier study compared the distance displaced by females marked at birth, to the distance displaced by a sample of males marked as adults at their breeding sites. An alternative explanation may be related to Marion Island being part of an island group, while Macquarie Island is isolated. It was assumed for the purposes of this study that Marion Island's neighbour, Prince Edward Island, did not affect the patterns of dispersal shown. The fact that males exhibit far greater site fidelity than females at Marion Island suggests that they are less likely to disperse to Prince Edward Island than females. The general pattern of dispersal, as related to sex, is thus unlikely to have been affected by the presence of Prince Edward Island. Assessing this would, however, require the tagging of a cohort of pups at Marion's neighbour.

Possible reasons for a female bias

Both male and female elephant seals at Marion Island disperse, and while the difference between the percentages breeding within one kilometre of their natal sites seems slight (22 % of males and 20 % of females) it is significant. This sex bias is contrary to the usual pattern of dispersal, both for mammals, and also for mammals showing mate defence polygyny (Greenwood 1980, Dobson 1982), such as elephant seals (Laws 1956a, Carrick *et al.* 1962a, McCann 1981). Female biased dispersal is typical rather, of a social system in which males defend territories. Amongst those few species of mammals showing the latter social system, males often cooperate with kin to defend a territory, and so remain in their natal territory. Females are therefore forced to disperse to avoid suffering the negative effects of inbreeding. However, where male biased dispersal is the norm, males usually defend access to mates rather than territory, and females must defend access to, and compete for resources. It is therefore of greater importance to the females, rather than to the males, to be philopatric (Greenwood 1980, Dobson 1982). As southern elephant seals fast during the breeding season, the only resources that female seals need at this time are breeding space and access to a mate. Neither is limited at Marion Island as harems only cover a very small portion of the space available (pers. obs.), and the numbers of adult males available are capable of inseminating all adult females (Wilkinson & Van Aarde 1999).

If philopatry leads to a substantial chance of inbreeding, then one of the sexes must disperse. Inbreeding is of less consequence to males in a social system as extremely polygynous as found in elephant seals. Successful males become beachmasters and father many pups. The loss of one or two as the result of inbreeding is of little consequence to them. Females, on the other hand, invest all their resources for a single year in one pup, and cannot risk an incestuous mating. Dispersal is a means of decreasing likelihood of such an event. To further assess the likelihood that inbreeding is important in explaining the female bias in southern elephant seal dispersal at Marion Island, it will be necessary to assess the probabilities of incest should animals breed at their natal site, and to determine whether the levels found are likely to be of consequence. A future study will show whether this is the case.

It is also possible that the difference in dispersal between males and females has less to do with competition and inbreeding than the migratory life history of elephant seals. The problems facing migratory animals, in terms of the selection of suitable sites or home ranges, are different to those of non-migratory animals. While non-migratory animals must expend energy and time on moving away from their natal site, and are therefore faced with the costs of dispersal (Morton 1992), these costs are negligible to migratory animals compared to the costs of migration. The difficulty facing migratory animals is, in contrast, returning to a previously used suitable site (Morton 1992, Paradis *et al.* 1998). The accuracy with which this is done is a compromise between the benefits attained from local familiarity and the costs due to time spent finding this site (Pärt 1991). It is possible that male elephant seals are able to spend more time moving between sites, and searching for a specific site during a haulout event. Male seals arrive earlier than females during the breeding season (Kirkman 1999). Moreover, females give birth soon after their arrival, after which time they are restricted to the site of parturition by virtue of the dependence of their pup. However, this is only a proximate reason for greater male site fidelity. The ultimate cause of the difference between the sexes must explain later female arrival during the breeding season. It is possible that this is related to the pregnant state of females arriving to breed, which may require them to forage for longer and consequently allows them to devote less time to finding a specific site. Furthermore, male and female elephant seals also appear to employ very different foraging strategies, by virtue of the species' great sexual dimorphism (Stewart & De Long 1993), and this may result in discrepancies in the amount of time that they are able to spend ashore during the breeding season.

6.3.2 Dispersion

No sex bias in moult dispersion is evident for southern elephant seals at the study site. The difference between the sexes for winter dispersion is most probably due to the different age structures of wintering animals of the two sexes. Elephant seals haul out to winter as immature animals, yet maturity is attained far later in males (six years) than females (three years). As will become evident in Chapter 7, age has a significant effect on the moult dispersion of southern elephant seals. When comparing uniform age groups of wintering animals (0 – 2 years of age), no significant difference is found between the two sexes.

These results are similar to those of other studies. Nichols (1970) found that, at Macquarie Island, immature elephant seals of both sexes had a similar tendency to return to their natal site for the winter. In considering moult dispersion of adult elephant seals at the Iles Kerguelen, Bester & Van Niekerk (1984) also found no differences between the sexes. The lack of sex-related differences is not surprising, as males and females appear to have similar requirements for non-reproductive haulout sites. Moulting seals of both sexes need access to moult wallows, and wintering immature animals appear to need little other than a beach of suitable topography on which to lie.

CHAPTER 7

FACTORS AFFECTING DISPERSAL AND DISPERSION

7.1 METHODS

Most female elephant seals at Marion Island start reproducing within the first six years of life (Bester & Wilkinson 1994, Pistorius *et. al.* 1999 a & b). It is possible that those few animals recorded breeding for the first time when older than six years had previously bred elsewhere, or are the result of incorrect tag reading (see Methods: assumptions). Data samples used for most investigations of natal dispersal by females were therefore restricted to individuals that bred for the first time at ages 3 – 6. Where this is not the case it is noted.

As there were far fewer records for males than for females, samples of male were not restricted by age for most tests.

7.1.1 Cohort

The samples were controlled for the effect of age to ensure that each cohort contained seals of the same range of ages. For females, the range of cohorts used were: for dispersal, 1983 – 1987 (ages 3 – 7), for moult dispersion, 1983 – 1987 (ages 1 – 6), and for winter dispersion, 1983 – 1989 (ages 0 – 4). For both natal and breeding dispersal by females, sample sizes of each cohort from 1983 to 1985 were 73 or less. The 1983 cohort for female winter dispersion only contained 65 individual haulout events.

Data were not restricted by age when assessing dispersal by males because of small sample size. The cohorts used were 1983 – 1986, and sample sizes varied from 8 to 19. For moult dispersion the cohorts used were 1983 – 1987 for ages 1 – 6, and for winter dispersion, 1983 – 1989 for ages 0 – 4.

7.1.2 Age

The range of age classes used varied widely among comparisons of females. Natal dispersal used ages 3 – 5 years, breeding dispersal, ages 4 – 7 years, moult dispersion, ages 1 – 7 years, and winter dispersion ages 0 – 2 years. The sample sizes of all classes, with the exception of moulting seven-year-olds (n = 74) were greater than 80.

The following age classes were used for males: for natal dispersal, 6 – 8 years, for breeding dispersal, 7 – 9 years, for moult dispersion, 1 – 6 years and 0 – 5 years for winter dispersion. Samples for dispersal all contained less than 34 individual haulouts events, for dispersion, only the moulting five-year-olds numbered less than 80 (n = 78).

7.1.3 Natal site isolation

Individuals from sites isolated by six km or more from neighbouring major parturition sites were excluded from analyses. For all movement by females and all dispersion by males, individual haulouts were separated into the following classes based on distance from natal site to the nearest major parturition site: 0 – 0,9 km, 1 – 1,9 km, 2 – 2,9 km and 5 – 5,9 km. Male dispersal data were divided into two classes, 0 – 2,9 km, and 3 – 5,9 km. All sample sizes for dispersal by males were smaller than eighty, while only one for females (5 – 5,9 km) was smaller than this number.

7.1.4 Natal site disturbance

Individuals born at sites exposed to very low levels of disturbance were excluded from analyses. All sample sizes for dispersal by males, and sample sizes from low disturbance sites for dispersal by females, numbered less than 80.

7.1.5 Natal harem size

All data for dispersal by females, and for natal dispersal by males, were grouped into three classes, based on the number of pups born in the individual's natal harem: 1 – 20 pups, 21 – 40 pups and 41 – 60 pups. Data for breeding dispersal by males were grouped into two classes: 1 – 30 pups and 31 – 60 pups. Seals born in harems in which more than 60 pups were born were excluded from analyses. The minimum sample size for female groups was 100 separate haulout events, while all groups of males contained less than 40 separate haulout events. For dispersion, data for both females and males were grouped into seven classes: 1 – 10 pups, 11 – 20 pups, 21 – 30 pups, 31 – 40 pups, 41 – 50 pups, 51 to 60 pups and 61-70 pups. The class, 61 – 70 contained fewer than 80 individuals for both males and females.

7.1.6 Pre-weaning mortality

Data for seals born in harems suffering six percent pre-weaning mortality or more were excluded from analyses. Other data for females were grouped into three samples: 0 – 1,9 %, 2 – 3,9 % and 4 – 5,9 %. Data for dispersion by males was classed in the same way, while data for dispersal by males was divided into the following two classes: 0 – 2,9 %

and 3 –5,9 %. All sample sizes for dispersal and dispersion by females, and for dispersion by males, were greater than 120. Sample sizes for dispersal by males did not exceed 30.

7.2 RESULTS

7.2.1 Natal dispersal

Cohort (natal dispersal)

No cohort of females (Kruskal-Wallis ANOVA H(4, n = 344) = 3,21, p = 0,52) or of males (Kruskal-Wallis ANOVA H(3, n = 65) = 2,56, p = 0,46) showed significantly greater, or lesser natal dispersal than any other.

Age (natal dispersal)

Amongst females breeding for the first time, five-year-olds hauled out significantly further from their natal site than three of four-year-olds (Kruskal-Wallis ANOVA H(2, n = 529) = 7,64, p < 0,05). There was no significant difference in natal dispersal between females aged three years and four years (Kolmogorov-Smirnov, p > 0,05), but a significant difference was apparent between three and five-year-olds (Kolmogorov-Smirnov, p < 0,05), and also between four and five-year-olds (Kolmogorov-Smirnov, p < 0,01) (Figure 7.1).

Age had no a significant effect on the dispersal of male elephant seals at Marion Island (Kruskal-Wallis ANOVA H(2, n = 77) = 1,42, p = 0,48), despite the apparent increase in the distance of dispersal with age (Figure 7.2).

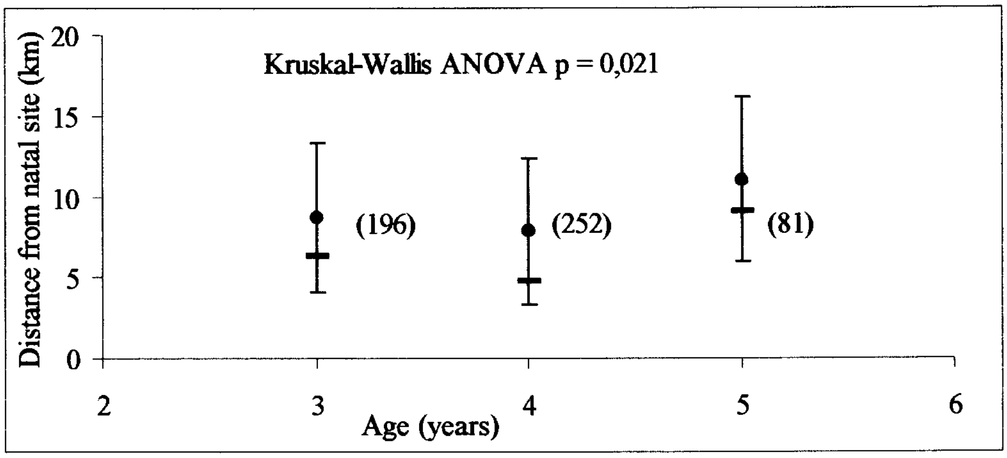

Figure 7.1 Mean distances (± half standard deviation) displaced between natal site and first reproductive haulout site by female southern elephant seals, *Mirounga leonina*, at Marion Island. The groups represent different age classes. The heavy horizontal bars indicate median values, while sample sizes are denoted in parentheses.

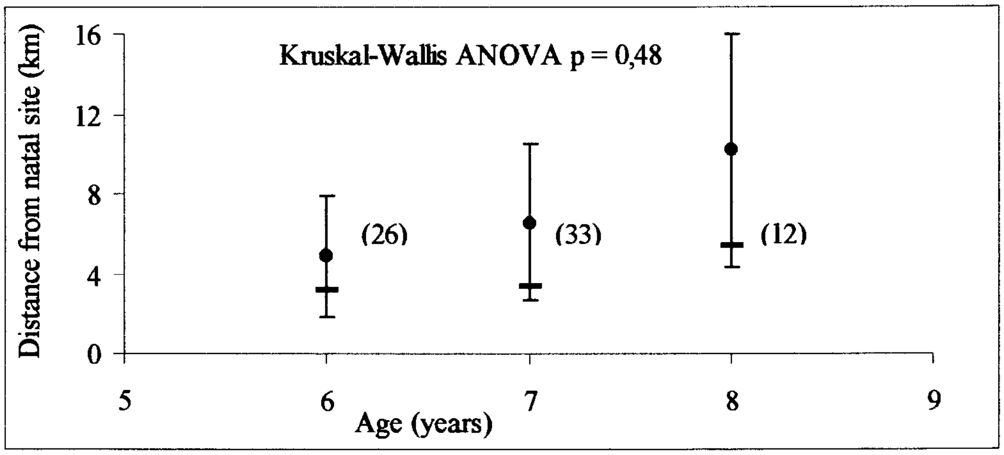

Figure 7.2 Mean distances (± half standard deviation) displaced between natal site and first reproductive haulout site by male southern elephant seals, *Mirounga leonina*, at Marion Island. The groups represent different age classes. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

Natal site isolation (natal dispersal)

Isolation of natal site had a highly significant effect on female natal dispersal (Kruskal-Wallis H (3, n = 563) = 15,92, p = 0,0012). Females born at beaches that lie between 5 – 6 km from the nearest major parturition site, dispersed further (x = 17,4 km) than those born at sites only one (x = 7,0 km), two (x= 8,5 km) or three km (x = 8,6 km) from a major parturition site (Figure 7.3). No significant difference due to natal site isolation was found for males (Kolmogorov-Smirnov, p > 0.05).

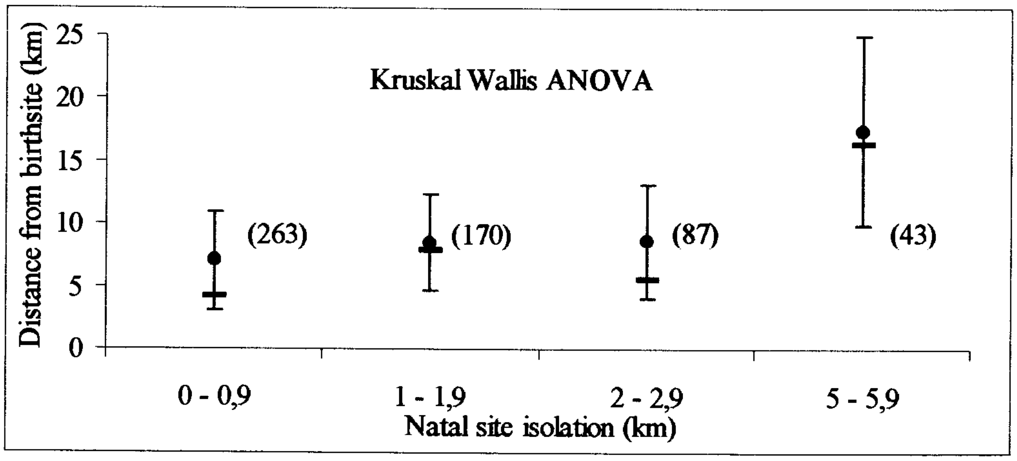

Figure 7.3 Mean distances (± half standard deviation) displaced between natal site and first reproductive haulout site by female southern elephant seals, *Mirounga leonina*, at Marion Island. The groups represent different levels of natal site isolation. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

Disturbance (natal dispersal)

The disturbance of a female seal's natal harem had a highly significant effect on it's natal dispersal (Kruskal-Wallis H (2, n = 562) = 13,63, p = 0.0011). Females born in harems exposed to low levels of human disturbance dispersed far further than did those exposed as pups to either medium or high levels of disturbance. A significant difference was also found between medium and high disturbance classes (Kolmogorov-Smirnov, $p < 0,01$), with seals born at sites exposed to high levels of disturbance dispersing further ($x = 8,3$ km) than those exposed to medium levels of disturbance ($x = 7,5$ km) (Figure 7.4). Therefore females of the medium disturbance class showed the least dispersal of the three classes.

No significant differences in dispersal were apparent for males (Kruskal-Wallis H (2, n = 82) = 1,29 p = 0,52).

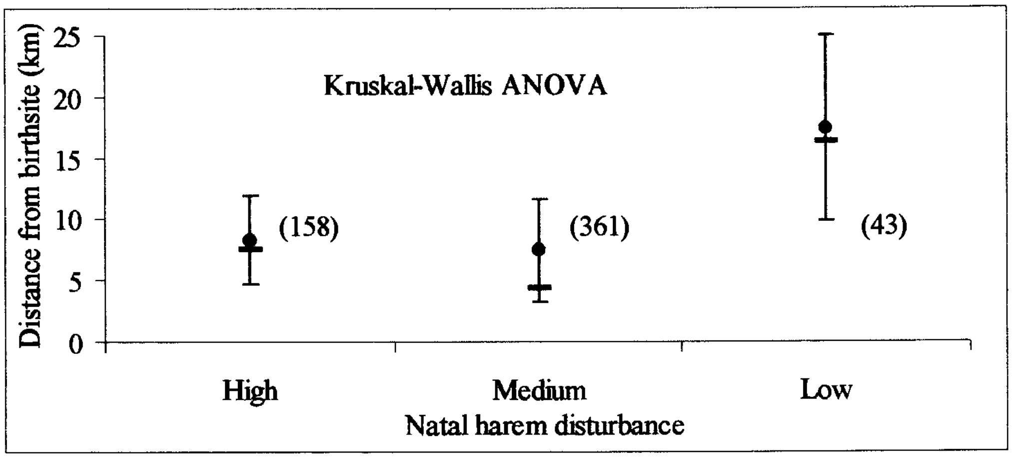

Figure 7.4 Mean distances (± half standard deviation) displaced between natal site and first reproductive haulout site by female southern elephant seals, *Mirounga leonina*, at Marion Island. The groups represent different levels of natal harem disturbance. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

Natal harem size (natal dispersal)

Size of natal harem had no significant effect on the natal dispersal of either female (Kruskal Wallis ANOVA H(2, n = 545) = 1,88, p = 0,39) or male (Kolmogorov-Smirnov, p > 0,05) elephant seals.

Pre-weaning mortality (natal dispersal)

No significant difference was found for the effect of pre-weaning mortality on natal dispersal of female (Kruskal-Wallis ANOVA H(2, n = 524) = 2,35, p = 0,31) or male (Kolmogorov-Smirnov, p > 0,05) elephant seals.

7.2.2 Breeding dispersal

Cohort (breeding dispersal)

No cohort of either females or males showed significantly different breeding dispersal to any other (Kruskal-Wallis ANOVA, Females: H(4, n = 309) = 3,41, p = 0,49, Males: H(3, n = 38) = 0.25, p = 0,97).

Age (breeding dispersal)

Age had no significant influence on the breeding dispersal of either female (Figure 7.5) (Kruskal-Wallis ANOVA H(3, n = 448) = 2,48, p = 0,48) or male (Kruskal-Wallis ANOVA H(2, n = 38) = 0,25 p = 0,97) elephant seals at Marion Island.

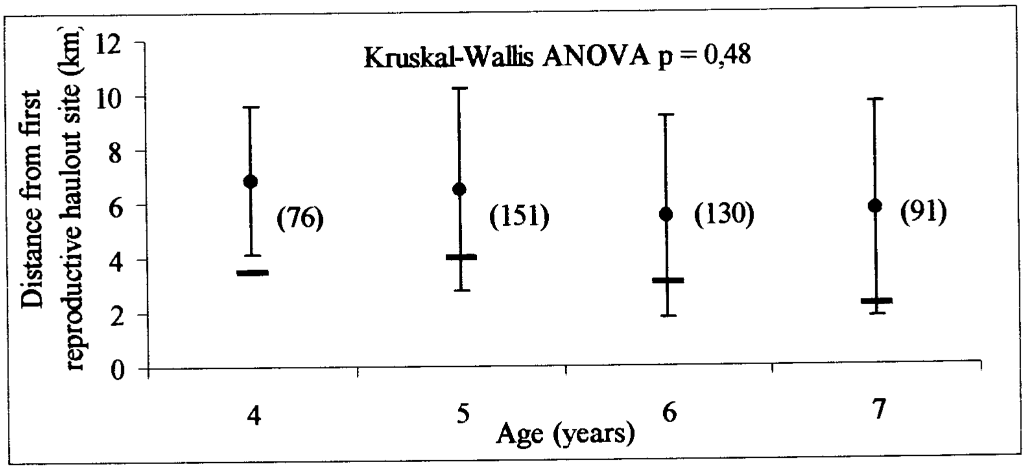

Figure 7.5 Mean distances (± half standard deviation) displaced between first and subsequent reproductive haulout sites by female southern elephant seals, *Mirounga leonina*, at Marion Island. The groups represent different age classes. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

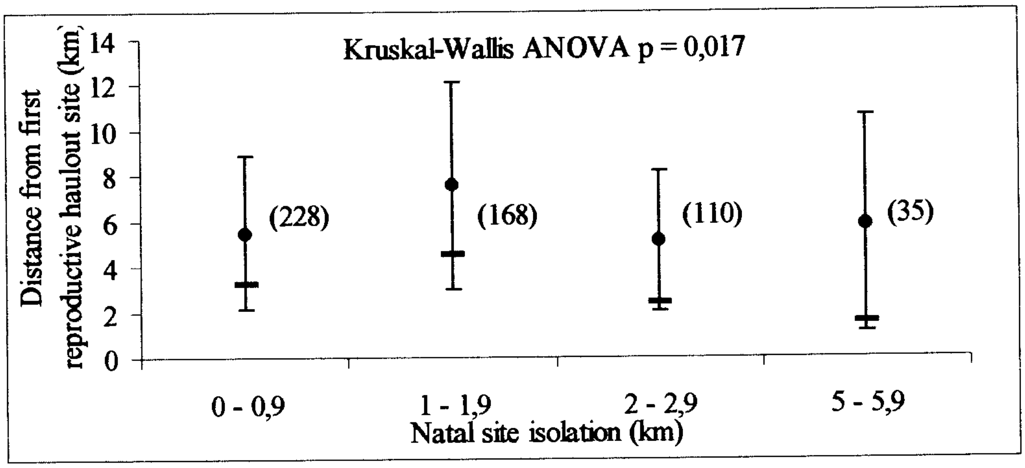

Figure 7.6 Mean distances (± half standard deviation) displaced between first and subsequent reproductive haulout sites by female southern elephant seals, *Mirounga leonina*, at Marion Island. The groups represent different levels of natal site isolation. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

Natal site isolation (breeding dispersal)

Isolation of natal site had a significant effect on the breeding dispersal of female seals (Kruskal-Wallis ANOVA H (3, n = 541) = 10.19, p = 0,017), although no pattern is evident (Figure 7.6). Seals born at sites isolated from neighbouring major parturition sites by 1 – 1,9 km of coastline showed greater breeding dispersal (x = 7,6 km) than those born at sites isolated by 0 – 0,9 km (x = 5,5 km), 2 – 2,9 km (x = 5,1 km) and 5 – 5,9 km (x = 5,8 km). No significant effect was found for males (Kolmogorov-Smirnov, p > 0,05).

Disturbance (breeding dispersal)

Disturbance had a highly significant effect on the breeding dispersal of female elephant seals (Kruskal-Wallis H(2, n = 541) = 10,85, p = 0,0044). Female seals born in harems exposed to high levels of human disturbance dispersed further (x = 7,2 km) from their first reproductive haulout than did those exposed to medium (x = 5,6 km) and low (x = 5,8 km) levels of disturbance (Figure 7.7) (Kolmogorov-Smirnov, p < 0,01 for both). There was also a slight, yet significant difference between medium and low disturbance harems (Kolmogorov-Smirnov, p < 0,05). Therefore, females from natal sites exposed to medium disturbance dispersed the shortest distances. Nevertheless, only 50 % of female elephant seals from high disturbance natal harems bred within 5 km of their first reproductive haulout site, compared to 66,3 % of females from medium disturbance harems, and 65,7 % of females from low disturbance harems. No significant differences due to natal harem disturbance were apparent for males (Kruskal-Wallis H (2, n = 41) = 0,34, p = 0,84).

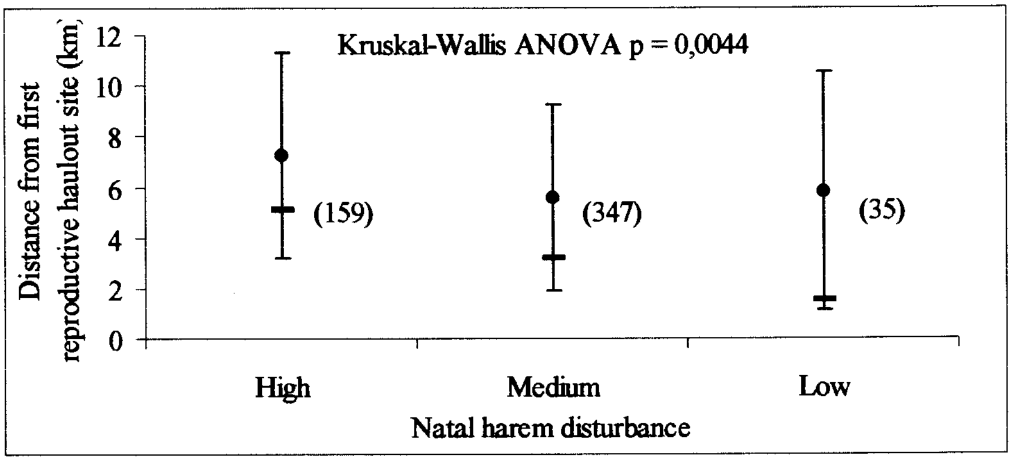

Figure 7.7 Mean distances (± half standard deviation) displaced between first and subsequent reproductive haulout sites by female southern elephant seals, *Mirounga leonina*, at Marion Island. The groups represent different levels of natal harem disturbance. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

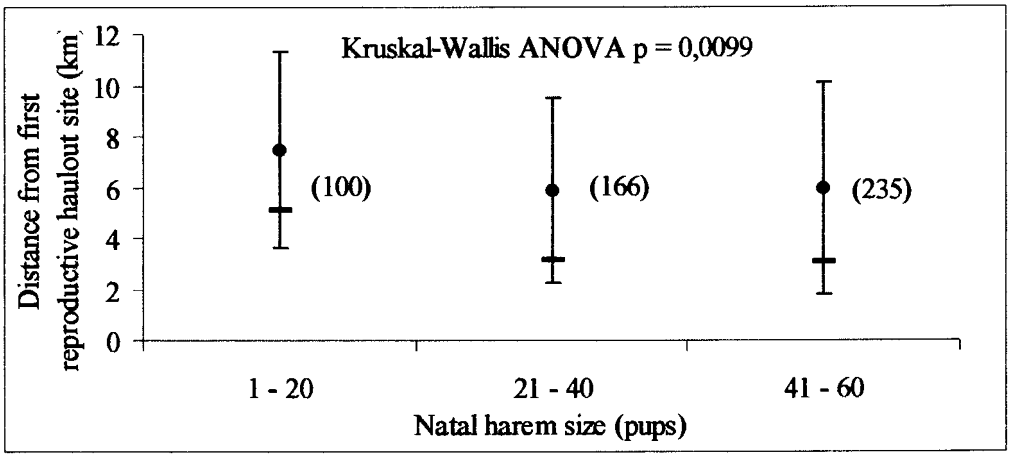

Figure 7.8 Mean distances (± half standard deviation) displaced between first and subsequent reproductive haulout sites by female southern elephant seals, *Mirounga leonina*, at Marion Island. The groups represent different natal harem sizes. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

Natal harem size (breeding dispersal)

Natal harem size had a significant effect on the breeding dispersal of female elephant seals (Kruskal-Wallis ANOVA H (2, n = 501) = 9,2, p = 0,0099) (Figure 7.8). Females born in smaller harems moved significantly further (x = 7,5) from their first reproductive haulout site when returning to breed than those from medium sized harems (x = 5,9) or large harems (x = 6,0) (Kolmogorov- Smirnov, p < 0,01 for both). No significant effect of natal harem size was apparent for breeding dispersal of male seals (Kolmogorov-Smirnov, p > 0.05).

Pre-weaning mortality (breeding dispersal)

Pre-weaning mortality had a significant effect on the breeding dispersal of female elephant seals (Kruskal-Wallis H (2, n = 502) = 16,09, p = 0,0003). Seals born at harems exposed to high pre-weaning mortality hauled out further from their first reproductive haulout site during subsequent reproductive haulouts than those who were born in harems where low levels of pre-weaning mortality were recorded (Figure 7.9).

Pre-weaning mortality does not have a significant effect on the dispersal of male elephant seals (Kolmogorov-Smirnov, n = 39, p > 0,05).

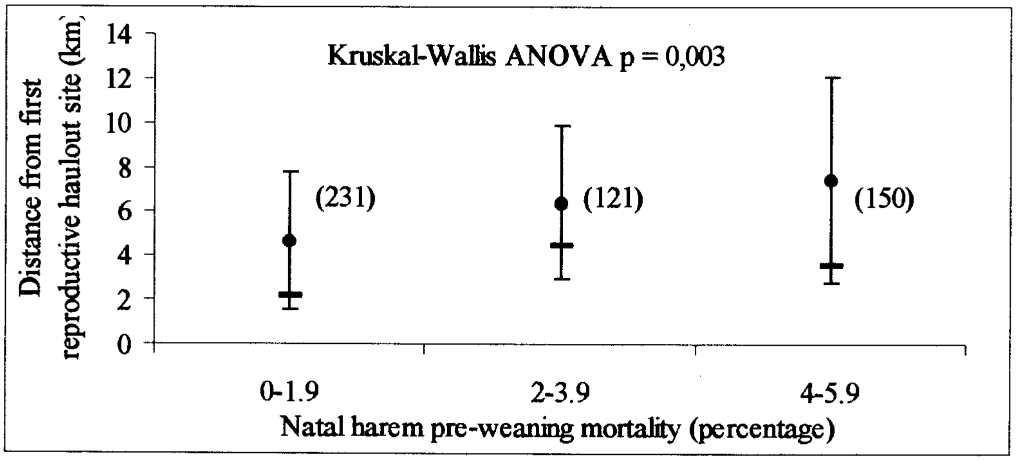

Figure 7.9 Mean distances (± half standard deviation) displaced between first and subsequent reproductive haulout sites by female southern elephant seals, *Mirounga leonina*, at Marion Island. The groups represent different levels of natal harem pre-weaning mortality. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

7.2.3 Moult dispersion

Cohort (moult dispersion)

Cohort had a highly significant effect on female moult dispersion (Kruskal-Wallis ANOVA H (4, n = 1719) = 19,9, p = 0,0005) although no pattern was readily discernible. Females born in 1986 hauled out significantly closer to their natal site (x = 7,9 km) than those born in 1983 (x = 10,2 km), 1985 (x = 11,1 km) or 1987 (x = 10,2 km) (in each case: Kolmogorov-Smirnov, p < 0,05) (Figure 7.10). Cohort had no significant effect on male moult dispersion (Kruskal-Wallis ANOVA H (4, n = 1440) = 3,11, p = 0.54).

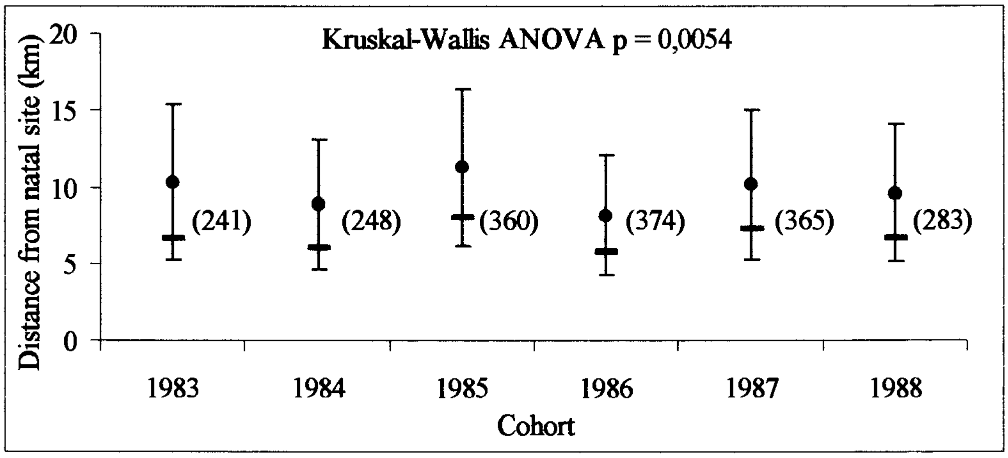

Figure 7.10 Mean distances (± half standard deviation) displaced from natal site by moulting female southern elephant seals, *Mirounga leonina*, at Marion Island. The groups represent different cohorts. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

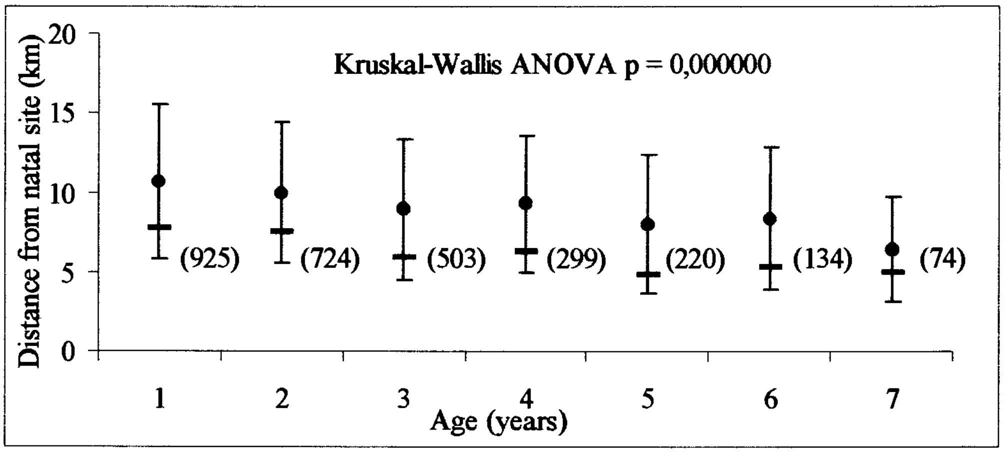

Figure 7.11 Mean distances (± half standard deviation) displaced from natal site by moulting female southern elephant seals, *Mirounga leonina*, at Marion Island. The groups represent different age classes. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

Age (moult dispersion)

Both females (Kruskal-Wallis ANOVA H(5, n = 1871) = 16,58, p = 0,0054) and males (Kruskal-Wallis ANOVA H(5, n = 2364) = 61,27, p = 0,0000) hauled out to moult significantly closer to their natal site with increasing age. The mean distance females were displaced decreased from the 10,7 km for yearlings, to the 6,4 km of seven-year-olds (Figure 7.11).

Male seals showed a very similar pattern, with yearlings having hauled out an average of 10, 5 km from their natal site, and six-year-olds, an average of 6,4 km (Figure 7.12).

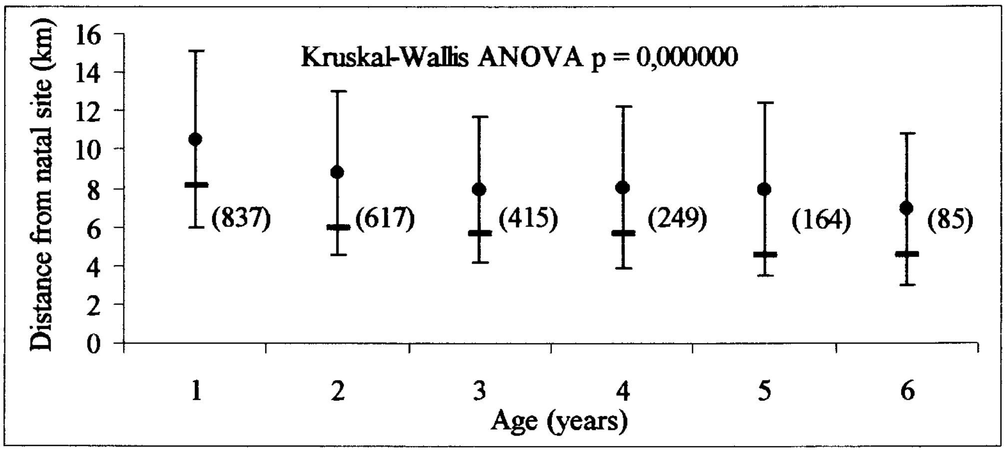

Figure 7.12 Mean distances (± half standard deviation) displaced from natal site by moulting male southern elephant seals, *Mirounga leonina*, at Marion Island. The groups represent different age classes. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

Natal site isolation (moult dispersion)

Seals born at isolated sites showed significantly greater moult dispersion than those born at less isolated sites (Females: Kruskal-Wallis ANOVA H(3, n = 2923) = 89,4, p = 0,0000; Males: Kruskal-Wallis H(3, n = 2429) = 11,2 p = 0,011). Female seals born at sites separated by 5 – 6 km from neighbouring major parturition sites, were displaced an average of 18,8 km from their natal site. This is more than twice the distance of the other categories (Figure 7.13). Males born at isolated sites also dispersed further (x = 14 km), though not quite double the distance of males originating at less isolated sites.

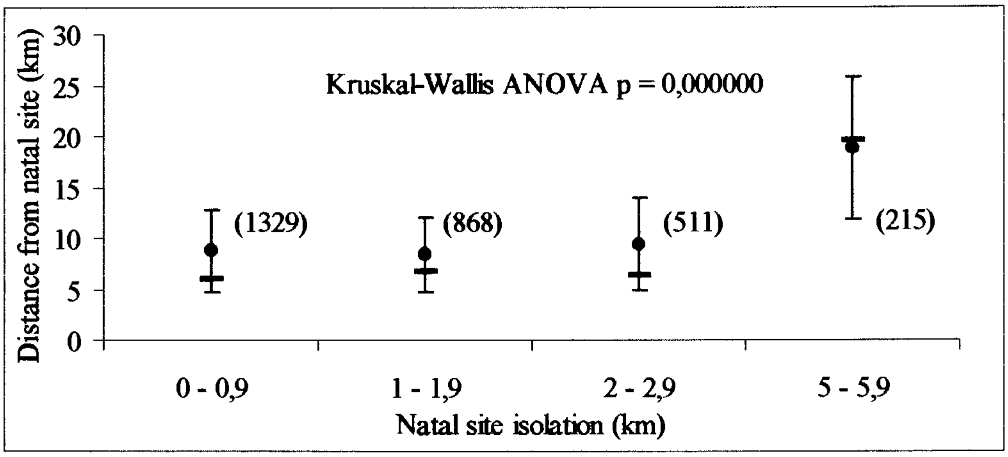

Figure 7.13 Mean distances (± half standard deviation) displaced from natal site by moulting female southern elephant seals, *Mirounga leonina*, at Marion Island. The groups represent different levels of natal site isolation. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

Disturbance (moult dispersion)

The level of disturbance of an elephant seal's natal harem had a highly significant effect on the distance dispersed to moult site for both females (Kruskal-Wallis ANOVA H(2, n = 2916) = 89,9, p = 00000) and males (Kruskal-Wallis ANOVA H(2, n = 2429) = 9,0, p = 0,011). For both sexes, animals exposed to low levels of disturbance moved far further from their natal site than animals exposed to medium and high levels of disturbance (Females: Figure 7.14). A significant difference also exists, however, between sites exposed to medium and high levels of disturbance (Kolmogorov-Smirnov, p < 0,01 for both females and males). Females born in harems exposed to medium disturbance dispersed an average of 8,9 km to moult sites, compared to 8,4 km for females from more disturbed harems. The results for males are similar, with those born in harems exposed to

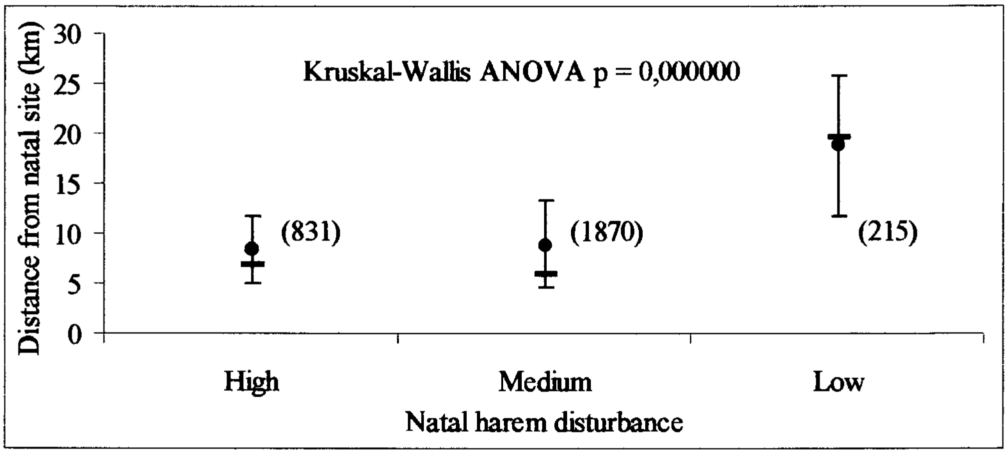

Figure 7.14 Mean distances (± half standard deviation) displaced from natal site by moulting female southern elephant seals, *Mirounga leonina*, at Marion Island. The groups represent different levels of natal harem disturbance by humans. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

high disturbance moulting, on average, a shorter distance (x = 7,5 km) from their natal site than those born in medium disturbance harems (x = 9,1 km).

Natal harem size (moult dispersion)

Natal harem size had a significant effect on the moult dispersion of male (Kruskal-Wallis ANOVA H(6, n = 2431) = 16,5 p = 0,011), but not female elephant seals (Kruskal-Wallis H(6, n = 2929) = 8,4, p = 0,21). Male seals born in harems of ≤ 10 pups moved significantly further (10,7 km) from their natal site than males born in larger harems (9,7 km) (Kolmogorov-Smirnov, p < 0,01 or p < 0,05) (Figure 7.15). Significant differences also existe between individuals born in harems of 11 – 20 and 21-30 pups, and individuals from harems of 41 – 50 and 51 – 60 pups (Kolmogorov-Smirnov, p < 0,05 in

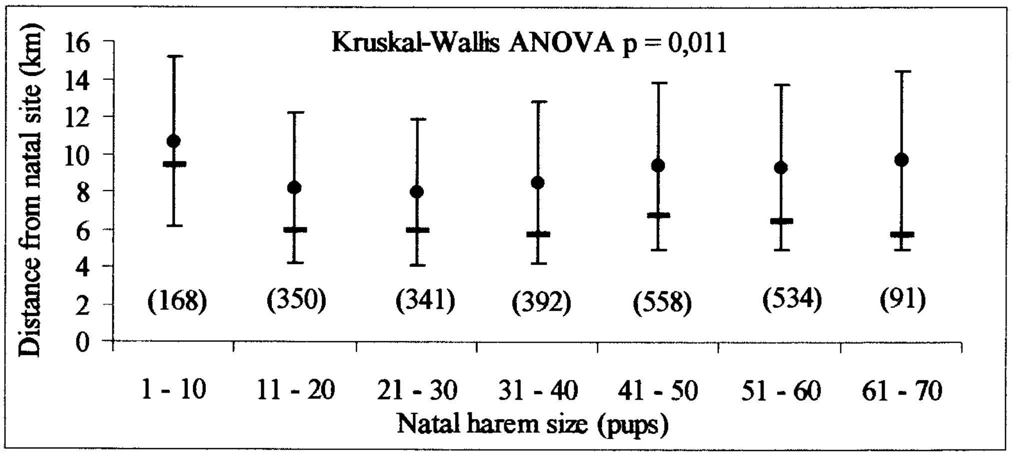

Figure 7.15 Mean distances (± half standard deviation) displaced from natal site by moulting male southern elephant seals, *Mirounga leonina*, at Marion Island. The groups represent different sizes of natal harems. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

all cases). In these cases though, it is the seals born in the larger harems, however, that dispersed further from their natal site than those born in smaller harems.

Pre-weaning mortality (moult dispersion)

Pre-weaning mortality levels have a significant effect on moult dispersion of both females (Kruskal-Wallis ANOVA H(2, n = 2739) = 6,3, p = 0,04) and males (Kruskal-Wallis ANOVA H(2, n = 2269) = 144,9, p = 0,0000). Animals from harems experiencing lower mortality dispersed further from their natal site. Females born in harems with low pre-weaning mortality dispersed an average of 10,3 km from their natal site, while females born in harems with medium levels of pre-weaning mortality dispersed an average of 8,9 km, and females from natal harems suffering high mortality, dispersed an

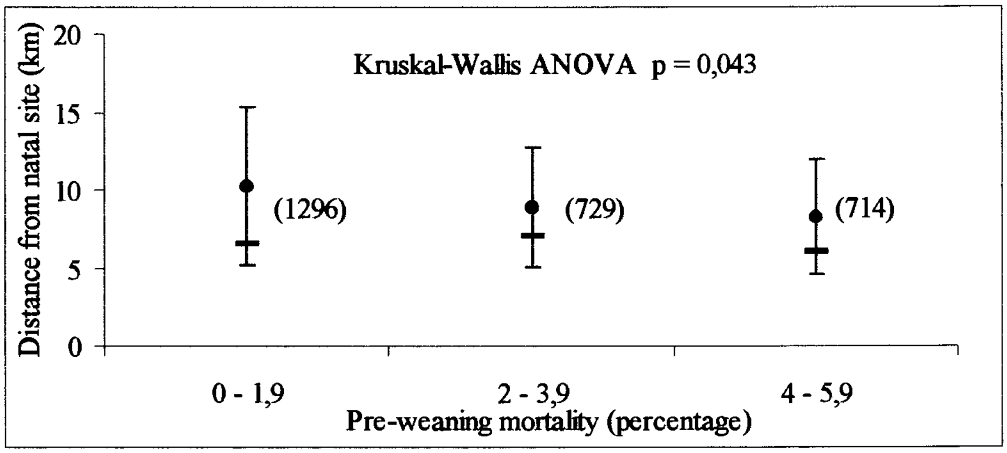

Figure 7.16 Mean distances (± half standard deviation) displaced from natal site by moulting female southern elephant seals, *Mirounga leonina*, at Marion Island. The groups represent different levels of natal harem pre-weaning mortality. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

average of 8,3 km (Figure 7.16). Males dispersed 10,1 km from low mortality harems, 8,0 km from medium mortality harems and 7,7 km from pre-weaning mortality harems.

7.2.4 Winter dispersion

Cohort (winter dispersion)

Cohort has a significant effect on the winter dispersion of male (Kruskal-Wallis ANOVA H(6, n = 1610) = 13,51, p = 0,037), but not female elephant seals (Kruskal-Wallis ANOVA H(6, n = 1268) = 11,65, p = 0,070). Male seals born during 1985 were displaced significantly further than those born during 1986, 1987 or 1989 (Kolmogorov-Smirnov, p < 0,05 in all three cases). The only pattern evident is that males from earlier cohorts dispersed further in winter than males from later cohorts (Figure 7.17).

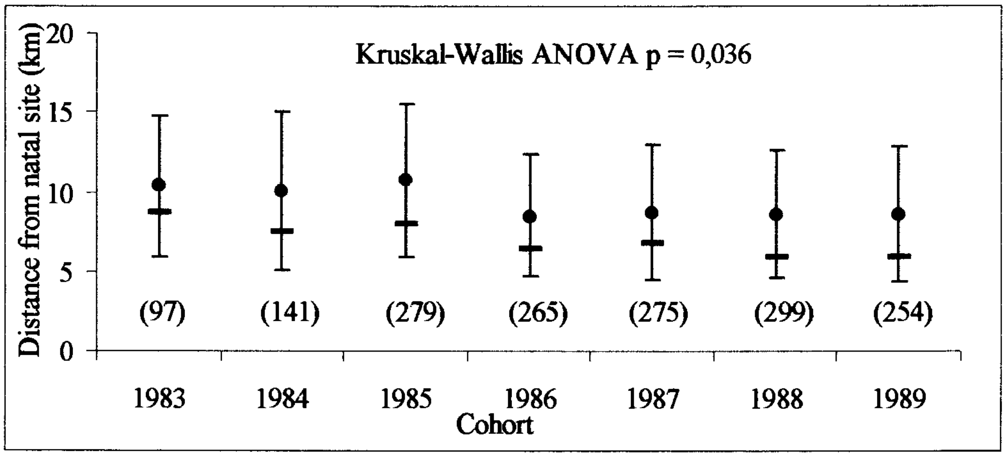

Figure 7.17 Mean distances (± half standard deviation) displaced from natal site by male southern elephant seals, *Mirounga leonina*, hauling out to winter at Marion Island. The groups represent different cohorts. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

Age (winter dispersion)

While no significant difference due to age is evident for female winter dispersion (Kruskal-Wallis ANOVA H(2, n = 1856) = 5,8, p = 0.054), male seals hauled out significantly closer to their natal sites as they aged (Kruskal-Wallis ANOVA H(5, n = 2369) = 68,2, p = 0,0000). Underyearling males wintered a mean distance of 10,8 km from their natal site. This distance decreased to an average of 6,4 km for five years old (Figure 7.18). Underyearlings dispersed significantly further from their natal site than all other age classes (Kolmogorov-Smirnov, p < 0,05 and 0,01). In addition yearlings dispersed significantly further than two-, three- and five-year-olds (Kolmogorov-Smirnov, p < 0,05 and 0,01).

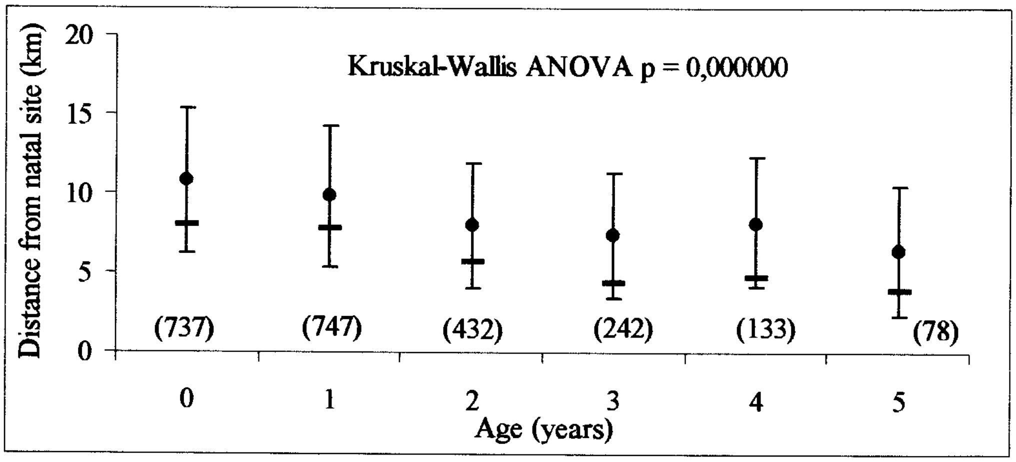

Figure 7.18 Mean distances (± half standard deviation) displaced from natal site by male southern elephant seals, *Mirounga leonina*, hauling out to winter at Marion Island. The groups represent different age classes. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

Natal site isolation (winter dispersion)

Female seals born on beaches located within three km of a major parturition site dispersed significantly shorter distances, to winter sites, than did females born on more isolated beaches (Kruskal-Wallis ANOVA H(3, n = 1954) = 126,3, p = 0,0000). Female seals from isolated sites dispersed a mean distance of 22,0 km, while those from less isolated sites dispersed mean distances of 10,1 km or less (Figure 7.19).

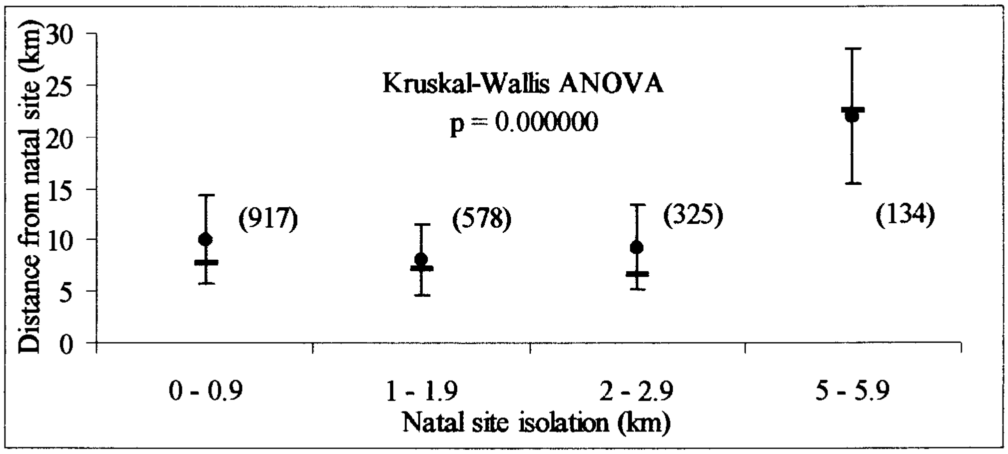

Figure 7.19 Mean distances (± half standard deviation) displaced from natal site by female southern elephant seals, *Mirounga leonina*, hauling out to winter at Marion Island. The groups represent different levels of natal site isolation. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

Male seals showed a similar significant pattern (Kruskal-Wallis ANOVA H(3, n = 2419) = 91,6, p = 0,0000). Males born at the most isolated sites (5 – 5,9 km) moved an average of 19,6 km from their natal site, compared to a maximum of 8,9 km by the other classes (Figure 7.20).

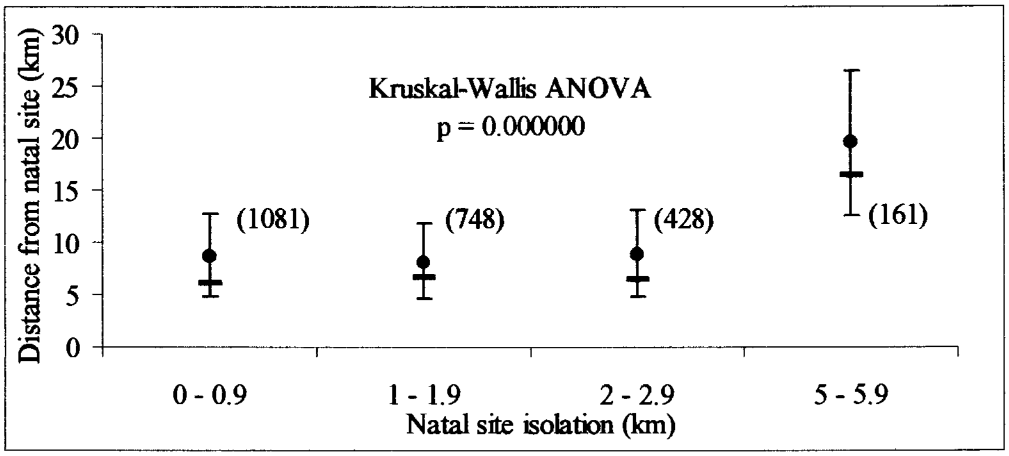

Figure 7.20 Mean distances (± half standard deviation) displaced from natal site by male southern elephant seals, *Mirounga leonina*, hauling out to winter at Marion Island. The groups represent different levels of natal site isolation. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

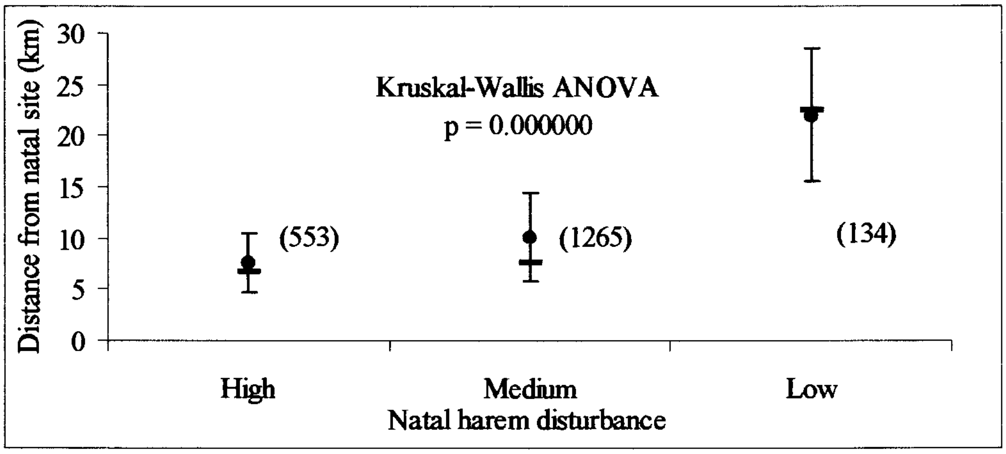

Figure 7.21 Mean distances (± half standard deviation) displaced from natal site by female southern elephant seals, *Mirounga leonina*, hauling out to winter at Marion Island. The groups represent different levels of natal site disturbance. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

Disturbance (winter dispersion)

Both female (Kruskal-Wallis ANOVA H(2, n = 1952) = 130,6, p = 0,0000) and male (Kruskal-Wallis ANOVA H(2, n = 2418) = 94,6, p = 0,0000) seals born in harems exposed to low disturbance dispersed significantly further from their natal site to winter sites, than those from harems exposed to medium or high disturbance (Figure 7.21). Females from low disturbance natal groups dispersed an average of 22 km from their natal site, which is more than double that of high (x = 7,6 km) and medium (x = 10,1 km) disturbance groups. The greater dispersal of females from medium disturbance harems compared to females from high disturbance harems is also significant (Kolmogorov-Smirnov, p < 0,01).

As with female seals, males from low disturbance harems dispersed more than twice the distance of males from more disturbed harems.

Natal harem size (winter dispersion)

Natal harem size has a significant effect on the winter dispersion of both females (Kruskal-Wallis ANOVA H(6, n = 1956) = 12,8, p = 0,046), and males (Kruskal-Wallis ANOVA H(6, n = 2422) = 16,6, p = 0,011). Seals born in smaller harems dispersed further than seals from larger ones. The mean distance of dispersal decreased with harem size from 11,2 km to 8,9 km for females (Figure 7.22), and from 11,2 km to 8,6 km for males.

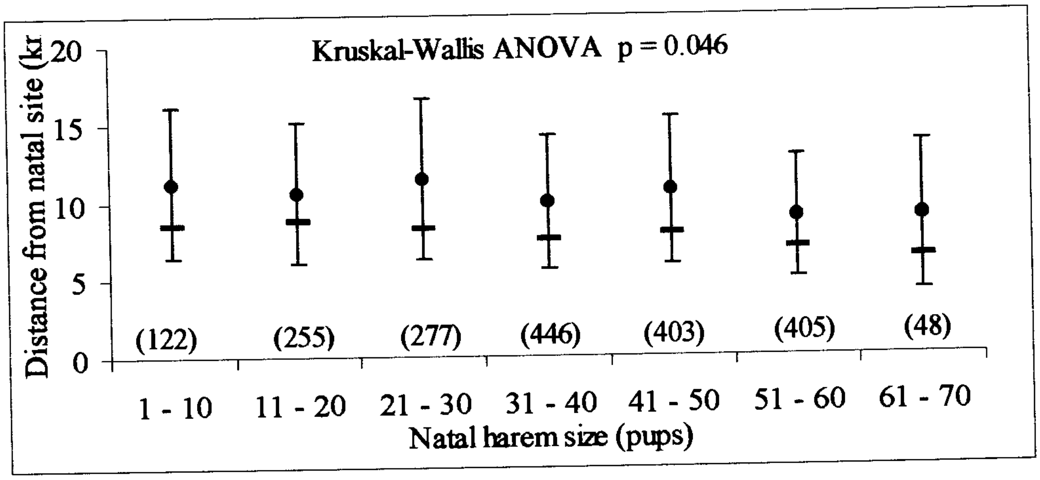

Figure 7.22 Mean distances (± half standard deviation) displaced from natal site by female southern elephant seals, *Mirounga leonina*, hauling out to winter at Marion Island. The groups represent different natal harem sizes. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

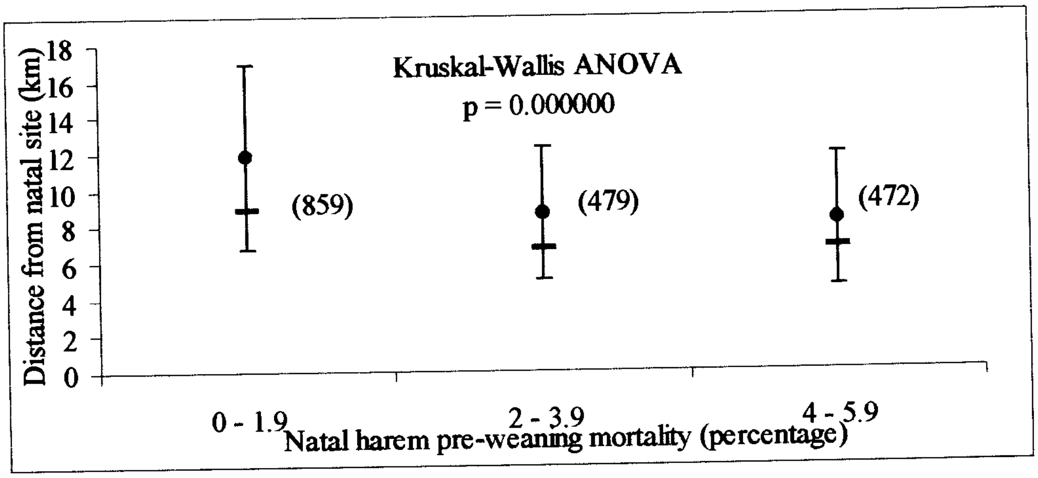

Figure 7.23 Mean distances (± half standard deviation) displaced from natal site by female southern elephant seals, *Mirounga leonina*, hauling out to winter at Marion Island. The groups represent different levels of natal harem pre-weaning mortality. The heavy horizontal bars indicate median values. Sample sizes are denoted in parentheses.

Pre-weaning mortality (winter dispersion)

High pre-weaning mortality is associated with a significantly lower winter dispersion distance for both females (Kruskal-Wallis ANOVA H(2, n =1810) = 35,4, p = 0,0000) and males (Kruskal-Wallis ANOVA H(2, n = 2277) = 22,4, p = 0,0000). Females born in harems exposed to low pre-weaning mortality (< 2 %) wintered a mean distance of 11,9 km from their natal site, compared to 8,7 km for females born in harems that experienced medium levels of pre-weaning mortality (2 – 3,9 %), and 8,3 km for females that experienced high levels of pre-weaning mortality (4 – 5,9 %) (Figure 7.23). For males, a similar pattern was demonstrated with those from low pre-weaning mortality harems dispersing an average of 10,5 km to their natal site, compared to averages of 8,1 km and 7,8 km for seals from harems experiencing higher pre-weaning mortality.

7.3 DISCUSSION

None of the factors assessed had any effect on either the natal or the breeding dispersal of male elephant seals, but results may be inconclusive due to the small sample sizes analysed. No conclusions can therefore be made with respect to male dispersal, which certainly warrants further study. This is now possible, as extra years of data have become available from the ongoing monitoring programme on Marion Island.

7.3.1 Does cohort have an effect on dispersal or dispersion?

Cohort seems to have little effect on any form of dispersal or dispersion of elephant seals at Marion Island. Only in the moult dispersion of females and the winter dispersion of males were any significant differences evident, but no pattern was apparent. In addition, no years characterised by high or low dispersion, whether significant or not, were found in common for any type of movement for either males or females. The conclusion must be that cohort has a negligible effect on dispersal or dispersion, at least for the time frame of this study, and for the data available. It is possible that with more years of data available, changes in dispersal or dispersion over time, and therefore with cohort will become evident.

Factors that have a temporally association may result in, either a gradual and directional change in the effect of cohort, or in single (or a few grouped) anomalous cohorts. A gradual change in dispersal or dispersion with cohort may be brought about by changes in population size. For instance, an increase in population size will theoretically result in an increase in dispersal due to greater competition for resources (Taylor & Taylor 1977, Dobson, 1979, Moore & Ali 1984). Studies of fur seals have demonstrated dramatic increases in numbers at (presumably) less suitable sites when population growth has slowed at neighbouring major sites (Payne 1977, Boyd 1993, Hofmeyr *et.al.* 1997). A portion of this increase is likely due to the immigration of individuals excluded from the more populous sites due to competition for space.

While elephant seals often haul out in very large and dense aggregations (Huber et al 1991) where effects such as competition for space are important (Stewart 1989), the relatively small aggregations typical of Marion Island (Wilkinson 1992) suggest that the influence of space is unimportant at this site. It follows that the lack of any density dependant effect on land may be responsible for the absence of any trend in dispersal or dispersion with time.

The isolated anomalous years identified in this study for some dispersion, may also be due to environmental factors, but ones specific to certain years. An extreme example of such an event would be the El Niño – Southern Oscillation (ENSO) of the Pacific Ocean (Trillmich & Ono 1991). Huber *et al.* (1991) indicated that effects of the 1982-83 ENSO on northern elephant seals were linked to cohort. No exceptional events were recorded for the duration of this study, but prior to its inception, in 1980, a volcanic eruption was recorded on the west coast of the island. The eruption resulted in a popular haulout site, Kaalkoppie Beach, becoming inaccessible to elephant seals (Verwoerd *et al.* 1981). While this site was predominantly a moult site (Panagis 1985), any elephant seals born there, would be expected to disperse further than normal in the year of the eruption.

The cohort effect on female moult, and male winter dispersion may be due to environmental events specific to single years. That the effects are sex specific is possibly related to the extreme sexual dimorphism shown by elephant seals (Le Boeuf & Laws 1994), which influences both their behaviour (Stewart & Delong 1994), and life history patterns (Kirkman 1999). Differences in foraging behaviour may leave one sex susceptible to influences that will not affect the other. Further, significant differences in the timing of events between the sexes (Kirkman 1999) could conceivably result in short-term events having a greater influence on whichever sex is more likely to be on land or at sea concurrent with that event.

Whatever the reasons are for the significant differences found, they cannot be adequately addressed by this study. They do, however, indicate an important avenue of research, particularily in light of the unexplained decline in the elephant seal population at Marion Island, and a number of other sites, in the past few decades (Condy 1978, Bester 1980, Skinner & Van Aarde 1983, Bester & Wilkinson 1994, Pistorius *et al.* 1999). Such an investigation would need to assess the connection between spatial and temporal effects of environmental factors (e.g. annual changes in the position of the Antarctic Polar Front), and behavioural parameters (e.g. timing of haulout and patterns of dispersal).

7.3.2 Age

Increases in site fidelity with age have been demonstrated for many species (Baker 1978). Seals are not unusual in this respect (Stirling 1974, Reiter *et al.* 1981, Testa 1987a, Huber *et al.* 1991, Baker *et al.* 1995). Few studies, however, have marked animals at birth and subsequently measured movement from natal site. Although Baker *et al.* (1995) made use of data from seals marked at their natal site, they did not differentiate between natal and breeding dispersal. Indeed, most studies make little distinction between the various types of dispersal or dispersion, concentrating instead on differences in movement between adults and immature animals. No previous studies of seals have considered the effect of age at first reproduction on natal dispersal, or have considered breeding dispersal alone.

Female natal dispersal

This study has shown that natal dispersal of female elephant seals at Marion Island was affected by age. Older females breeding for the first time, hauled out further from their natal site than younger individuals. It has been suggested that the length of absence from a site influences the accuracy with which an animal returns to that site (Morton 1992). Possibly, female seals breeding for the first time at a greater age will be less familiar with the exact location of their natal site than younger females, and thus less likely to return there. Baker *et al.* (1995) suggested that the greater philopatry that they demonstrated for female compared to male northern fur seals, was because males were less familiar with their natal site by virtue of their greater age of first reproduction. In contrast, male elephant seals at Marion Island were more philopatric than females, despite being older at first breeding.

Female breeding dispersal

Age had no effect on the breeding dispersal of female elephant seals at Marion Island. Pomeroy *et al.* (1994) did not observe any change in the breeding dispersal of female grey seals with increasing number of years between marking as breeding adults, and resighting in subsequent breeding seasons. Although their results were not directly related to age, of importance is that both female grey seals and southern elephant seals (this study) disperse little between consecutive breeding sites.

It is logical that, if reproduction is successful, there is no reason for an animal to haul out at another breeding site, during subsequent reproductive events. It is also possible that breeding dispersal does not decrease with age, because seals, on average, cannot navigate back to their first reproductive site with any greater accuracy despite the number of visits to a site.

Dispersion

Fidelity to natal site increases with age for both sexes for both moult and winter dispersion. This trend was not significant only for female winter dispersion, possibly as a result of the limited number of age classes (three) available for comparison. Many other studies have shown greater movement from natal site by immature seals compared to adults (Stirling 1974, Reiter *et al.* 1981, Croxall & Hiby 1983, Bjørge & McConnell 1986, Testa 1987a, Borsa 1990, Huber *et al.* 1991, Rounsevell & Pemberton 1994). In a study of southern elephant seals at the Iles Kerguelen, Bester & Van Niekerk (1984) recorded greater moult dispersion by immature elephant seals compared to adults.

A number of factors may contribute to a decrease in the distance of dispersal with age:

1. Less competition for space, as the temporal separation between the breeding season and the moult of immatures increases with age.
2. The greater accuracy of return for reproductive haulouts may influence the accuracy of other haulouts.
3. Increased local familiarity with age, leading to an improved ability to find a specific site.

Immature elephant seals are vulnerable in aggressive interactions with older animals, especially bachelor males during the breeding season (pers. obs.). Yet there is considerable overlap in the timing of the moult haulout by immatures and the breeding season (Kirkman 1999). This overlap is reduced with increasing age of the immature seals (Kirkman 1999), which would reduce the chance of interaction with breeding adults. It follows that there would be less cause for older immature animals to disperse from their natal site. This line of reasoning does not hold for the effect of age on the winter haulout, however, despite a negligible overlap with the breeding season.

Decreasing distance of dispersion with age may be associated with greater philopatry of breeding season haulouts by adults. Once seals have reached adulthood and show considerable site fidelity during breeding haulouts, they may continue to show greater site fidelity during the moult. However, the decrease in dispersion does not occur only after maturity, but starts a number of years before.

Increased site fidelity with age could result from increased familiarity with the areas surrounding the natal site. Pärt (1995) explained the higher philopatry in older collared flycatchers (*Fecedula albicollis*), as being due to the increasing benefits of prior local experience with age. It is possible that with every return to Marion Island elephant seals improve in their ability to recognise features that will enable them to navigate to their natal site.

7.3.3 Natal site isolation

Southern elephant seals from Marion Island show far less site fidelity when born at more isolated sites. This is true for reproductive, moult and winter haulouts. The results imply that elephant seals generally are unable to find the exact site of their birth, and often haul out in its vicinity. If seals born at isolated sites were unable to find their natal site, they would be forced to haul out far further away. The results also indicate that there is more movement between sites if they are located close to one another, as has been demonstrated for northern elephant seals (Leboeuf *et al.* 1974, Huber *et al.* 1991) and for many species of migratory seabirds (Weimerskirch & Jouventin 1987, Aebischer 1995).

7.3.4 Natal harem disturbance

It must be noted that the effect of disturbance considered here is disturbance at the seal's natal site. In retrospect it may have been more beneficial to consider the effects of disturbance at sites used as an adult. However, since elephant seals at Marion Island are highly philopatric (see Chapter 4), it seems reasonable to assume that they will experience similar levels of disturbance throughout their life.

A curious pattern emerges when considering the possible effects of human disturbance on dispersal and dispersion: seals born at sites exposed to low disturbance disperse further than seals born at more disturbed sites. This is easily explained if one notes that all sites visited less often by humans are also the sites that are the most isolated. The effect of natal harem disturbance is thus confounded by site isolation. Excluding all sites isolated by more than three kilometres also excludes all sites of low disturbance.

When comparing sites of high and medium disturbance only, the patterns of dispersal and dispersion remain difficult to explain. Seals born at sites exposed to high disturbance showed a greater degree of philopatry when hauling out for the moult or winter than seals born at site exposed to medium disturbance. Yet females born at high disturbance natal sites move further to breed than those from medium disturbance sites. In summary, seals hauling out for non-reproductive purposes move far from less disturbed sites, while seals hauling out for reproduction move far from more disturbed sites. The latter result makes sense and has been shown in studies of animals as dissimilar as badgers, *Meles meles*, (Cheeseman *et.al.* 1988) and greater flamingos, *Phoenocpterus rubber* (Nager *et.al.* 1996). Presumably, the quality of the site of reproduction is more important than sites used for other purposes. Thus, it is logical that reproductive sites are more carefully chosen than non-reproductive sites. It follows that non-reproductive sites should be less affected by disturbance. Possibly, those sites in the more disturbed areas are more suitable, for reasons unrelated to disturbance, for the moult and winter haulouts. Quick glance at the relative popularities of each of these sites indicates that this may well be the case. While only 24,4 % of seals breeding on the island, breed within the high disturbance area, some 28, 6 % of seals, moult within this area, and 32,1 % of seals haul out for the winter within this area.

7.3.5 Natal harem size

The popularity of a site used for reproduction by colonial animals could possibly be an indication of the quality of that site, and also, the quality and quantity of mating partners available at that site (Aebisher 1995). It follows that animals should be attracted to large breeding aggregations, and should breed there unless excluded by more adept competition for limited resources. Studies of wandering albatrosses, *Diomedea exulans*, (Weimerskirch & Jouventin 1987) and kittiwakes, *Rissa tridactyla*, (Porter & Coulson 1987) have indicated that the attractiveness of a breeding site for colonial seabirds increases with its the size and density.

While natal harem size has no effect on female natal dispersal, it does so on breeding dispersal, with animals born in small harems (≤ 20 pups) dispersing further than animals from larger harems. With regard to dispersion, only for moult dispersion by females does natal harem size not have a significant effect, although the pattern shown is very similar to the patterns of female winter dispersion and all male dispersion. For the winter and the moult, animals from smaller harems (10, 20 or 30 pups or less) disperse further.

The effect of natal harem size on dispersal and dispersion is not gradual for elephant seals from Marion Island. Seals born in harems of 10 or less, or 20 or less pups disperse further than those from born in larger harems, but there is no difference in dispersal between seals born in different size classes of harems of more than 20 pups.

It is possible that the effect of size on dispersal and dispersion may be due to seals being attracted to more populous sites, either because popularity is an indication of site quality, or because seals may haul out where they are more likely to have observed other seals. Seals born in smaller harems would therefore be less likely to haul out at their natal site compared to those born in large harems.

7.3.6 Natal harem pre-weaning mortality

While the various classes of pre-weaning mortality may seem to differ little in percentage (0 – 1,9 %, 2 – 3,9 % and 4 – 5,9 %), the effect of this difference on dispersal and dispersion was significant. Pre-weaning mortality had an effect both on dispersion of southern elephant seals at Marion Island, and also on the breeding dispersal of female seals.

The effects of pre-weaning mortality described are on an animal at its site of birth. As with natal harem disturbance, it would have in retrospect been of greater benefit to assess the effect of the pre-weaning mortality at a seal's site of reproduction on site fidelity.

Factors responsible for high natal harem pre-weaning mortality need not result only in the death of a higher than average percentage of pups, but may also affect the survivors by influencing their condition. Pre-weaning mortality could therefore be seen as a measure of the quality of the pre-weaning environment. It is possible that it influences dispersal and dispersion in one of two ways: (1) seals incur a permanent physical disadvantage, affecting their ability to navigate by reducing the amount of energy they are able to invest in finding their natal site, and (2) the fact that a natal site is of poor quality leads a seal to avoid it when returning to breed.

It is impossible to assess the validity of the first hypothesis in this thesis. Such an investigation would require assessing the condition of pups as related to their environment, and an assessment of how permanent that condition is, and its influence on behaviour.

If the second hypothesis were true, levels of pre-weaning mortality should have an effect on natal dispersal, and not on breeding dispersal. However, it is the breeding dispersal of southern elephant seals at Marion Island that is affected, while natal dispersal is not influenced. This indicates that, either the quality of the site at which the seal was born does not affect the choice of its first breeding site, or that the levels of pre-weaning mortality found at Marion Island were insignificant in this regard.

Another possible effect of the quality of a site, as measured by pre-weaning mortality is related to the proven philopatry of southern elephant seals (see chapter 4). Southern elephant seals are likely to breed where they are born, a may therefore expose their pups to conditions similar to those that they experienced prior to weaning. This has repercussions for the adult seal's reproductive success. Animals that lose a pup due to the poor quality of their first reproductive haulout site would be expected to disperse further when returning to breed than successful mothers. Many studies have shown that reduced breeding success, or breeding failure leads to greater breeding dispersal (Catchpole 1972, Beletsky & Orians 1978, Newton & Marquiss 1982, Bensch & Hasselquist 1991, Reed & Oring 1993, Aebischer 1995, Nager *et.al.* 1996). The increased breeding dispersal with increased natal harem pre-weaning mortality of elephant seals at Marion Island may therefore be due to the effect of poor reproductive success of incipient breeders at sites that also happen to be their natal sites. This may indicate that low breeding success leads to greater dispersal in the subsequent year. The link is tenuous, however, and will require future work to assess the effect of breeding site quality on breeding dispersal.

Should pre-weaning mortality have an effect on dispersion? Possibly not. As there is little to suggest that the choice of moult or winter site is directly linked to reproductive success, it follows that site quality should have little effect on dispersion distances. Nevertheless, there is the curious effect of elephant seals on Marion Island dispersing further from their natal site if they were born at sites of low pre-weaning mortality. This appears counter-intuitive and is difficult to explain. The answer may lie in the relationship between the pre-weaning mortality and the relative popularity of sites for reproduction, moulting and winter. The pattern that emerges is that sites of high pre-weaning mortality are more popular as moult and winter sites than sites of low pre-weaning mortality. The ratio of reproductive to moult popularity at low pre-weaning mortality sites (0 – 2,9 % mortality) is 1: 0,64. At high pre-weaning mortality sites (4 – 5,9 % mortality) it is 1: 0,8. A similar pattern is evident for winter sites. The ratio between reproductive and winter popularity for low pre-weaning mortality sites is 1: 0,6, but for high pre-weaning mortality sites it is 1:1,06. It appears that the reason that seals born at low pre-weaning mortality sites disperse further to moult and to winter is because they are selecting moult and winter sites, and that these sites happen to be ones characterised by higher levels of pre-weaning mortality. A possible reason for this selection is discussed in the conclusion.

CHAPTER 8

CONCLUSION

This study focused on the movements of southern elephant seals at Marion Island in relation to their natal site and site of first reproduction. The results give an indication of the relevance of various factors associated with the seals' choice of haulout site, and therefore their use of the terrestrial environment.

8.1 Cohort and effect of the environment

Cohort had no effect on dispersal or dispersion, except on the winter haulout by males and on the moult haulout by females. However, no pattern was apparent for these two exceptions, and it seems that cohort is either not of relevance when considering dispersal and dispersion, or that the time frame of the present study is too short to detect changes in behaviour resulting from changes in cohort. Cohort-linked behavioural changes may be an indication of the effect of temporal variability of the environment, and investigation of these changes may give insight into the factors influencing population changes. This is especially important in light of the decline that the Marion Island elephant seal population, amongst others, has been subject to over the past few decades.

8.2 Quality of haulout site

Three factors related to the quality of the site were found to affect the patterns of dispersal and dispersion and therefore, possibly the choice of haulout site. These were anthropogenic disturbance levels at the natal site, natal pre-weaning mortality and natal harem size. The latter two factors may be indirect measures of site quality.

The data indicate that elephant seals born in small harems (< 20 pups) dispersed further than those born in larger harems whether the seals came ashore to reproduce, to moult or during the winter. An explanation may lie in the possible attraction of seals to more populous sites, either because the number of seals at a site is an indication of its quality, or because the seals were simply hauling out where they were more likely to observe other seals. Therefore, seals from smaller harems would be more likely to haul out at sites other than their natal site, compared to seals from larger harems.

Breeding seals tended to disperse further from sites exposed to higher levels of onshore anthropogenic disturbance, and from sites that may have suffered higher levels of pup mortality. While the pre-weaning mortality levels of a site may affect reproductive success, and cause seals to disperse to another site for subsequent reproductive haulouts, the effect of disturbance may be more direct (though of less impact): seals may relocate after disturbance if they have yet to give birth or assume dominance of a harem.

Disturbance and pre-weaning mortality had the opposite effect on dispersion, with seals from less disturbed sites and sites of lower pup mortality moving further. However, the data indicate that these sites are also more popular moult and winter sites. It may be that the very attraction of these sites to seals hauling out to moult and during the winter is the avoidance of them by breeding adults. There is a substantial temporal overlap between the moult by immature seals and the breeding season. Immatures may avoid the disturbance and possible dangers associated with breeding aggregations by hauling out at sites less popular with breeding adults. Evidence against this hypothesis is the similar effect of disturbance and pre-weaning mortality on both moult and winter dispersion, despite no temporal overlap between the winter haulout and the breeding season.

However, it is possible that immature seals have learned to avoid sites popular with adults.

A corollary to the above hypothesis is that while disturbance has sufficient impact to cause greater dispersal of breeding seals, it may be of less consequence to immature seals than the disturbance and danger associated with breeding harems. Furthermore, Wilkinson and Bester (1988) demonstrated that onshore anthropogenic disturbance was not responsible for the decline in the elephant seal population at Marion Island, implying that while disturbance may affect dispersal and dispersion, it has little or no effect on actual reproductive success.

8.3 Isolation of the natal harem

Effects of natal harem isolation are apparently the most straightforward and the easiest to account for. Seals born at isolated sites show comparatively little fidelity to them, perhaps indicating that few seals are able to navigate to their natal site with great accuracy, instead often returning to the vicinity of the natal site. Where there are no other sites in the vicinity, as is the case for isolated sites, a seal that does not find its natal site will be forced to disperse further.

8.4 Age and the differences between various types of dispersal and dispersion

This study indicates that, while immature elephant seals show a significant level of fidelity to their natal site, they are less philopatric than adults. This pattern is at least partially due to immature seals hauling out for non-reproductive purposes only, while adults also haul out to breed. Furthermore, the mean distances of dispersion to non-reproductive sites are less than mean dispersal distances. The difference in site fidelity between dispersal and dispersion of elephant seals may result from moult and winter haulouts being more tenuously linked to reproductive success, when compared to reproductive haulouts. The choice of moult and winter sites would therefore be of less consequence than the choice of breeding sites. However, it may be that moult and winter sites are chosen on the basis of criteria unimportant to breeding seals, resulting in movement away from the natal site during dispersion.

Immatures also show less site fidelity than adults because dispersion distances decline with age. As noted above, immature elephant seals may avoid the disturbance and danger associated with breeding aggregations by dispersing away from popular breeding areas, one of which may be their natal site. Furthermore, the temporal overlap between the breeding season and the moult haulout decreases with age to the point where adult seals haul out to moult some time after the end of the breeding season.

Age also affects natal dispersal by females, with older incipient breeders hauling out further from their natal site than younger ones, possibly because familiarity with a site may decline with increasing length of absence from that site. However, males show greater fidelity to their natal site than females, despite the greater temporal discontinuity between birth and first breeding, although it may be that other factors explain greater male philopatry, and these are discussed below.

8.5 Sex bias in dispersal and dispersion

The sex bias in dispersal and dispersion apparent for elephant seals at Marion Island is unusual when compared to the sex bias found for most other mammals, and also for most other animals showing mate defence polygyny, and is not easily explained. However, the female bias in dispersal demonstrated for elephant seals at Marion Island is possibly linked to the apparent absence of competition between females, at this location, for resources at breeding sites. An absence of competition would reduce the benefits accruing from familiarity with local resources, relative to the costs of inbreeding. The net benefits to females would therefore be less than the net benefits to males, and this ratio would be different to that of other animals showing mate defence polygyny.

Sex bias in site fidelity may have less to do with familiarity with resources and the effects of inbreeding than with aspects of the disparate life histories of males and females, specifically with regard to the amount of time they are able to invest in finding their natal site. Male seals haul out earlier than females during the breeding season and may therefore have more time to search for a specific site. Moreover, females give birth soon after their arrival, after which they are unable to move between sites. This is, however, only a proximate reason for sex bias. The later arrival of females may be due to their pregnancy, which might require them to forage for longer, and would consequently allow them to devote less time to finding a specific site.

8.6 A synthesis

The results of this study suggest the following account of, and explanation for, the movements of southern elephant seals in relation to their life history. Many of the proposed hypotheses are speculative and will require further research:

1. Immature elephant seals hauling out to moult and for the winter, return to the vicinity of their natal site so as to remain familiar with their natal region. However, they

avoid breeding beaches because of the associated disturbance and danger, which has a direct effect during the moult, where this avoidance is learned. Having learned to avoid breeding beaches during the moult they also do so for winter haulouts.

2. As the immature seals grow and are less affected by the disturbance of the breeding season, because of the increasing temporal separation between breeding and moult haulouts, they move closer to their natal site or to more popular haulout sites.
3. Elephant seals haul out to breed for first time in their region of familiarity, but actively seek, either their natal site, or a popular breeding site. Older incipient breeding female seals are less familiar with the region of their natal site and therefore do not haul out as close to their natal site as do younger seals.
4. The seals return with great accuracy to the site of first reproduction on subsequent reproductive haulouts, because the absence of a mere year between reproductive haulouts does not reduce familiarity with that site. This accuracy of return is possibly affected by reproductive success.
5. Adults haul out to moult close to their natal site because they are familiar with its location, through breeding in its vicinity.

8.7 Directions for future research

This study suggests the following questions, if the truth of many of the above statements are to be assessed:

1. What is the effect of environmental variability on the timing of haulouts, on dispersal and on the survival of animals in different sex and age classes and different cohorts?
2. What is the pattern of spatial use of the terrestrial environment by southern elephant seals of different age and sex classes, hauling out for reproduction, moulting and the winter, in relation to the characteristics and quality of sites?
3. What are the patterns of movement between sites during one haulout event by different age and sex classes of southern elephant seals during the breeding season, during the moult and during the winter haulout, and how does this affect their choice of haulout site?
4. What is the outcome of behavioural interactions between different age and sex classes of southern elephant seals at different times of the year?
5. What levels of inbreeding would result from complete philopatry by all seals, and would these levels be of consequence to the seals?
6. Do southern elephant seals show fidelity to any previous haulout sites other than their natal site and their site of first reproduction, during subsequent haulouts?
7. Are there any major differences in the patterns of dispersal between the various populations of southern elephant seals, and what factors are likely to be responsible for these differences?

SUMMARY

1. This study focused on the movements of southern elephant seals in relation to natal site and site of first reproduction.

2. An extensive database of records of resights of southern elephant seals at Marion Island, that were collected during a programme of regular resighting over a period of twelve years, were used to generate frequency distributions of dispersal distances. These distributions were used to compare the effects of various factors on male and female seals.

3. Expected values of dispersal and dispersion were calculated from a probability matrix that considered all possible distances of movement between sites and the relative site popularity for breeding, moult and winter haulouts.

4. Both male and female elephant seals hauled out to breed closer to their natal site than was expected by chance alone. Two hypotheses may be relevant in explaining this: (1) familiarity with a site, or region, may be of benefit during breeding, and (2) the seals' own survival is proof that their natal site is suitable as a site of reproduction.

5. Both male and female elephant seals hauled out closer to their site of first reproduction than was expected by chance alone, when returning to breed in subsequent years, possibly because a successful reproductive season is an indication that the site used during that season will be suitable for future reproduction.

6. Both male and female elephant seals hauled out to moult, and for the winter, closer to their natal site than was expected by chance alone, possibly to maintain familiarity with the area of their natal site which would assist them in locating it in future years.

7. Both male and female southern elephant seals at Marion Island hauled out closer to their site of first reproduction than to their natal site, during reproductive haulouts subsequent to the first. Two hypotheses may be relevant in explaining this: (1) by not breeding at the exact location of their natal site, seals may have already avoided the negative consequences of philopatry and therefore do not need to disperse further, and (2) the shorter period of absence between consecutive breeding haulout events compared to the period between birth and first reproduction, may result in greater familiarity with the site of first reproduction.

8. Both male and female southern elephant seals showed no difference between moult and winter dispersion, possibly because most sites at Marion Island provide the requirements for both of these types of haulout.

9. Both male and female southern elephant seals at Marion Island hauled out closer to their natal site to breed than to moult or for the winter. Three hypotheses may be relevant in explaining this: (1) the choice of sites used for moult and winter haulouts are not as important as the choice of sites of reproduction because they are not directly linked to reproductive success, (2) moulting immature seals, (whose haulouts overlap temporally with the

breeding season) wish to avoid the disturbance and danger of popular breeding sites, and (3) seals hauling out to moult and for the winter are seeking sites on the basis of characteristics that are not of importance for breeding seals.

10. The small difference between the sexes, for both natal and breeding dispersal, was found to be significant, with females being the predominant dispersers. This pattern is unusual both for mammals and animals showing mate-defence polygyny (such as elephant seals). Two factors may be relevant in explaining this: (1) the low benefits for females from site fidelity (since female elephant seals do not compete for resources at Marion Island during breeding) and the higher costs of inbreeding for females compared to males in a polygynous system, or (2) the later arrival of female seals during the breeding season, compared to males, and the fact that the females give birth within a few days of their arrival, allow them less time to move between sites and therefore search for, and move closer to, a specific site.

11. No sex bias was found for either moult or winter dispersion, possibly because male and female seals do not differ in their requirements for sites used during non-reproductive haulouts.

12. The sizes of samples for dispersal by males were too small to determine the significance of the effect of various factors.

13. Apart from the presence of a number of unexplained and unusual isolated cohorts for moult dispersion by females and winter dispersion by males, no effect of cohort could be detected.

14. The distance of natal dispersal by female seals increased with age of first reproduction, possibly because of a greater length of absence from the natal site reduced familiarity with that site.

15. Age had no effect on the breeding dispersal of female seals, possibly because they were already returning to their site of first reproduction with maximum accuracy.

16. Moult and winter dispersion distances decreased with increasing age. While the decrease for winter dispersion is unexplained, two hypotheses may be of relevance in explaining the reduction in moult dispersion with age: (1) as the temporal overlap between the moult haulout of immatures and the breeding season decreases with increase in age, there is less of a need for moulting seals to avoid popular breeding haulouts, or (2) the greater familiarity with increasing number of visits to a site increases the accuracy with which a seal locates a site.

17. Elephant seals from isolated sites moved far further from their natal site for both dispersal and dispersion, possible as a result of the lack of neighbouring beaches for seals to haul out at should they not find the exact location of their natal site.

18. Levels of disturbance, pre-weaning mortality and the size of the natal harem may act, either by influencing seals in such a way as to modify their behaviour later in life, or by being the factors that those seals meet with at later haulout sites, by virtue of their fidelity to their natal sites.

19. Seals from harems exposed to higher disturbance dispersed further to breed, possibly because they are likely to move away from sites where they encounter humans, and not necessarily because of any effect on reproductive success.

20. Seals from harems exposed to less disturbance dispersed further to moult and when hauling out during the winter. Furthermore, the more disturbed sites are more popular as moult and winter sites. It is possible that non-reproducing immature seals select sites exposed to greater human disturbance because they are avoided by breeding adults and therefore the immatures are able to avoid the disturbance and danger associated with the breeding season.

21. Seals born in small harems (<20 pups) dispersed further for breeding, moult and winter haulouts than those from bigger harems, possibly because site popularity is an indication of site quality, or because more populous sites are more noticeable.

22. Breeding female seals born at sites of high pre-weaning mortality dispersed further than those from sites of low pre-weaning mortality, possibly because the factors leading to high pre-weaning mortality negatively affected seals at their natal site, or at their sites of reproduction even if they did not lose a pup.

23. Moulting seals, and seals hauling out for the winter born at sites of low pre-weaning mortality, dispersed further than seals from sites of high pre-weaning mortality. Furthermore, the high pre-weaning mortality sites are more popular as moult and winter sites. It is possible that non-reproducing immature seals select these sites because they are avoided by breeding adults and therefore are able to avoid the disturbance and danger of the breeding season.

24. The many hypotheses posed to explain the characteristics of dispersal and dispersion indicate a number of directions for future research. Amongst these are: (1) the effect of variation in the environment on dispersing behaviour, (2) investigations into the spatial use of the terrestrial environment, (3) the effect of interactions between seals on their choice of site, (4) the patterns of movements during haulout events, (5) the probability of inbreeding, assuming complete philopatry, (6) the effect of previous haulout site other than the natal site on dispersal and dispersion, and (7) the differences in patterns of dispersal between different populations.

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APPENDICES

APPENDIX 1: GLOSSARY

Adult Age class of females that have hauled out to breed, or males that have reached their sixth birthday.

Autumn-winter haulout Haulout during autumn and winter during which a considerable number of immature seals come ashore for an unknown purpose, possibly to rest. It extends from March to the end of August.

Bachelor Adult male elephant seal having hauled out during the breeding season but not controlling mating access to at least two adult females.

Beachmaster Adult male elephant seal that controls mating access to at least two adult females during the breeding season.

Breeding dispersal Movement from the site at which reproduction was first attempted to subsequent sites of attempted reproduction.

Breeding haulout Haulout during which female seals give birth to, and suckle their pups, and mate, and during which males compete for access to breeding females and mate. The breeding season typically extends from early August to mid-November.

Dispersal The movement of individual animals from their natal site to a site, or sites where reproduction (mating or parturition) is attempted.

Dispersion The long-term movements of an individual animal to sites where reproduction is not attempted.

Foraging trip Period of time spent at sea between haulout events and assumed to be of at least 30 days duration.

Extended study area Portion of the coastline of Marion Island from Storm Petrel Bay, around to the east, to Kildalkey Bay, and also Watertunnel Beach and Goodhope Bay East.

Haulout Period spent ashore.

Haulout event Entire period spent ashore in between extended foraging trips at sea. Short intervals in the sea, usually of only a few hours duration during this time are not important. During one haulout event the seal may haulout, and therefore, be recorded at several sites.

Immature Age class including all pups, underyearlings, yearlings, and subadults but excluding all adults.

Major parturition site A site at which a harem almost certainly exists during the breeding season. Specifically, a site at which 90 or more pups were born from 1983 - 1994.

Migration Regular seasonal movements between home ranges.

Moult haulout Haulout during which seals haul out to lose their old their old hair and outer layer of skin. The moulting season typically extends from early November to late April.

Natal dispersal The movement of an animal from its natal site to the site of first attempted reproduction.

Philopatry Return to natal site for the purposes of reproducing.

Post weaning haulout Period spent ashore by weaned pups prior to their first extended pelagic phase.

Primary haulout record Record of a haulout by a seal that defines the major site used by that seal during one haulout event.

Pup Age class of elephant seals from birth up to the time of first extended foraging trip.

Site Portion of coastline at which seals can haul out.

Study area Portion of the coastline of Marion Island from Ship's Cove to Archway Beach.

Subadult Age class of elephant seals that have reached two years of age but, in the case of females, have yet to haul out to breed, and in the case of males, have not yet reached their seventh birthday.

Underyearling Age class of seals in their first year, but which have left land for their first extended foraging trip.

Yearling	Age class of seals in their second year.

APPENDIX 2: EXAMPLES OF INDIVIDUAL DATA RECORDS

Table A2.1 All recorded haulout events for the female southern elephant seal, *Mirounga leonina*, tag number Blue 080, from Marion Island. The site codes are given in Appendix 3.

Age	Type of haulout	Site	Distance from natal site (km)
0	Birth	056	0,0
1	Moult	057	1,0
1	Winter	060	2,5
2	Moult	004	12,3
2	Winter	055	0,7
3	Moult	055	0,7
4	Breeding	064	4,7
4	Moult	066	7,3
5	Breeding	007	13,8
5	Moult	057	1,0
6	Breeding	058	1,6
6	Moult	057	1,0
7	Breeding	056	0,0
7	Moult	057	1,0
8	Moult	058	1,6
9	Breeding	063	3,7
10	Breeding	056	0,0

Table A2.2 All recorded haulout events for the male southern elephant seal, *Mirounga leonina*, tag number Orange 031, from Marion Island. The site codes are given in Appendix 3.

Age	Type of haulout	Site	Distance from natal site (km)
0	Birth	001	0,0
1	Moult	056	9, 5
1	Winter	067	1,4
2	Moult	002	1,3
3	Moult	065	3,8
4	Moult	002	1,3
5	Moult	001	0,0
6	Moult	007	4,3
6	Winter	007	4,3
7	Breeding	007	4,3
7	Moult	002	1,3
8	Breeding	001	0,0
8	Moult	002	1,3
9	Breeding	002	1,3
9	Moult	001	1,0
10	Breeding	002	1,3
10	Moult	002	1,3

APPENDIX 3: A LIST OF SITES ON MARION ISLAND

Table A3.1 Southern elephant seal haulout sites at Marion Island. Entries in bold type are classified as major parturition sites (m.p.s.). Disturbance is a relative measure of disturbance based on the number of times sites are visited per month by observers.

Code	Beach	Distance to nearest (other) m.p.s. (km)	Disturbance 1983-91	Disturbance 1992-94
001	Boulder Beach	1.3	High	High
002	Trypot Beach	1.6	High	High
003	Macaroni Bay, North	0.4	High	High
004	Macaroni Bay, South	1.5	High	High
005	Macaroni Bay, Rocks	0.1	High	High
006	Archway Bay	0.2	High	High
007	Archway Beach	1.5	High	High
008	East Cape	1.3	Moderate	Moderate
009	Hansen Cove	1.9	Moderate	Moderate
010	Tiny Beach	-	Moderate	Moderate
011	Bullard Bay, North	0.3	Moderate	Moderate
012	Bullard Bay, South	0.3	Moderate	Moderate
013	Killer Whale Cove	1.4	Moderate	Moderate
014	Waterfall Beach	0.3	Moderate	Moderate
015	Landfall Beach	0.8	Moderate	Moderate
016	Sealer's Cave	0.8	Moderate	Moderate
017	Whale Bird Point	1.0	Moderate	Moderate
018	Funk Bay	1.0	Moderate	Moderate

Appendix 3 continued.

Code	Beach	Distance to nearest (other) m.p.s. (km)	Disturbance 1983-91	Disturbance 1992-94
019	Kildalkey Rocks	0.5	Moderate	Moderate
020	Kildalkey Bay	1.0	Moderate	Moderate
021	Hooker Cove	-	Very low	Very low
022	Cape Hooker	-	Very low	Very low
023	Puisie Beach	-	Very low	Very low
024	Crawford Bay	-	Very low	Very low
025	Watertunnel Beach	5.1	Low	Moderate
026	Goodhope Bay, East	5.1	Low	Moderate
027	Goodhope Bay, West	0.8	Very low	Very low
028	Rooks Peninsula	-	Very low	Very low
029	Rooks Bay, East	-	Very low	Very low
030	Rooks Bay, West	-	Very low	Very low
031	Vrystaat Point	-	Very low	Very low
032	Cape Crozier	-	Very low	Very low
033	La Grange Kop	12.0	Very low	Very low
034	Swarkop Point	16.3	Very low	Very low
035	Swartkop – Kaalkoppie	-	Very low	Very low
036	Kaalkoppie Beach	-	Very low	Very low
037	Kaalkoppie – Sickle Cove	-	Very low	Very low
038	Sickle Cove	-	Very low	Very low
039	Sickle Cove – Fur Seal Bay	-	Very low	Very low
040	Fur Bay Bay	-	Very low	Very low

Appendix 3 continued.

Code	Beach	Distance to nearest (other) m.p.s. (km)	Disturbance 1983-91	Disturbance 1992-94
041	Fur Seal Peninsula	-	Very low	Very low
042	Mixed Pickle Cove	-	Very low	Very low
043	Mixed Pick. – Triegaardt B.	-	Very low	Very low
044	Triegaardt Bay	-	Very low	Very low
045	Triegaardt B. – Cape Davis	-	Very low	Very low
046	Cape Davis, Sealer's Beach	8.3	Very low	Very low
047	Cape Davis, Cliff Beach	-	Very low	Very low
048	Cape Davis, Steep Beach	-	Very low	Very low
049	Lou-se-Kop	-	Very low	Very low
050	Boot Rock Cove	-	Very low	Very low
051	Storm Petrel Bay	2.6	Moderate	Moderate
052	Storm Petrel B. - Goney B.	1.3	Moderate	Moderate
053	Goney Bay	2.2	Moderate	Moderate
054	Goney Bay – Log Beach	0.6	Moderate	Moderate
055	Log Beach	0.7	Moderate	Moderate
056	King Penguin Bay	1.6	Moderate	Moderate
057	King Peng. B. – Pinnicle B.	0.6	Moderate	Moderate
058	Pinnacle Beach	0.9	Moderate	Moderate
059	Sea Elephant Bay	0.2	Moderate	Moderate
060	Blue Petrel Bay	0.9	Moderate	Moderate
061	Blue Petrel B. – Sealer's B.	-	Moderate	Moderate
062	Sealer's Beach	1.0	Moderate	Moderate

Appendix 3 concluded.

Code	Beach	Distance to nearest (other) m.p.s. (km)	Disturbance 1983-91	Disturbance 1992-94
063	Sealer's South	0.3	Moderate	Moderate
064	Sealers South – Ship's Cove	1.0	Moderate	Moderate
065	Ship's Cove	2.3	High	High
066	Duiker's Point	1.6	High	High
067	Rockhopper Bay	2.4	High	High
068	Van den Boogard Beach	1.7	High	High

APPENDIX 4: POPULARITY VALUES OF ALL BEACHES FOR REPRODUCTIVE, MOULT AND WINTER HAULOUTS

Table A4.1 Percentages of tagged and untagged southern elephant seals, *Mirounga leonina*, recorded during regular censuses from 1990 - 1995 at each site on Marion Island for each haulout type, and the percentage of pups tagged at each site from 1983 - 1994.

Site	Reproduction	Moult	Winter	Tagged pups
051	0.1	0.8	1.0	0.2
052	0.06	1.2	0.9	0.03
053	8.2	4.9	5.8	8.8
054	0.07	0.6	0.7	0.02
055	0.5	2.1	1.6	0.4
056	6.9	5.3	5.8	8.2
057	0.6	2.1	1.2	0.2
058	4.2	1.9	2.9	4.9
059	0.5	1.4	1.0	0.4
060	3.2	2.1	1.4	3.2
061	0.1	0.3	0.3	0
062	6.5	4.3	3.0	8.2
063	1.8	2.0	2.5	1.0
064	0.7	2.9	3.0	0.4
065	6.1	4.9	4.3	7.3
066	0.2	1.5	1.1	0.06
067	0.7	2.9	4.4	0.9

Appendix 4 concluded.

Site	Reproduction	Moult	Winter	Tagged pups
068	0.03	0.09	0.2	0.03
001	0.3	2.9	4.1	0.4
002	5.6	4.6	5.5	6.7
003	0.05	0.06	1.0	0.05
004	3.6	3.1	4.8	4.1
005	.03	0.3	0.3	0.03
006	0.06	0.8	0.4	0.1
007	7.7	6.1	6.0	8.6
009	0.3	2.0	1.5	0.2
010	0.07	0.7	1.3	0
011	5.1	3.8	4.8	4.0
012	1.9	1.1	1.0	1.8
013	0.7	2.0	2.3	0.9
014	0.2	0.4	0.9	0.3
015	2.3	4.6	4.5	1.5
016	3.7	2.5	3.2	3.1
017	0.02	0.1	0.1	0
018	9.5	6.9	6.5	6.9
019	0.2	0.9	0.9	0.1
020	9.9	6.2	5.8	9.0
025	3.3	5.3	2.6	2.5
026	5.0	2.5	1.2	5.3

APPENDIX 5: FIT OF ELEPHANT SEAL DATA TO STANDARD DISTRIBUTION FREQUENCIES

Table A5.1 Fit of dispersal and dispersion data for female southern elephant seals, *Mirounga leonina*, at Marion Island to various standard distributions. Values are for X^2 tests. The following abbreviations are used for the various distributions: Norm. – normal, Exp. – exponential, Gam. – gamma, Logn. – log-normal, Chi-sq. – chi-squared, Bin. – binomial, Pois. – poisson, Geom. – geometric.

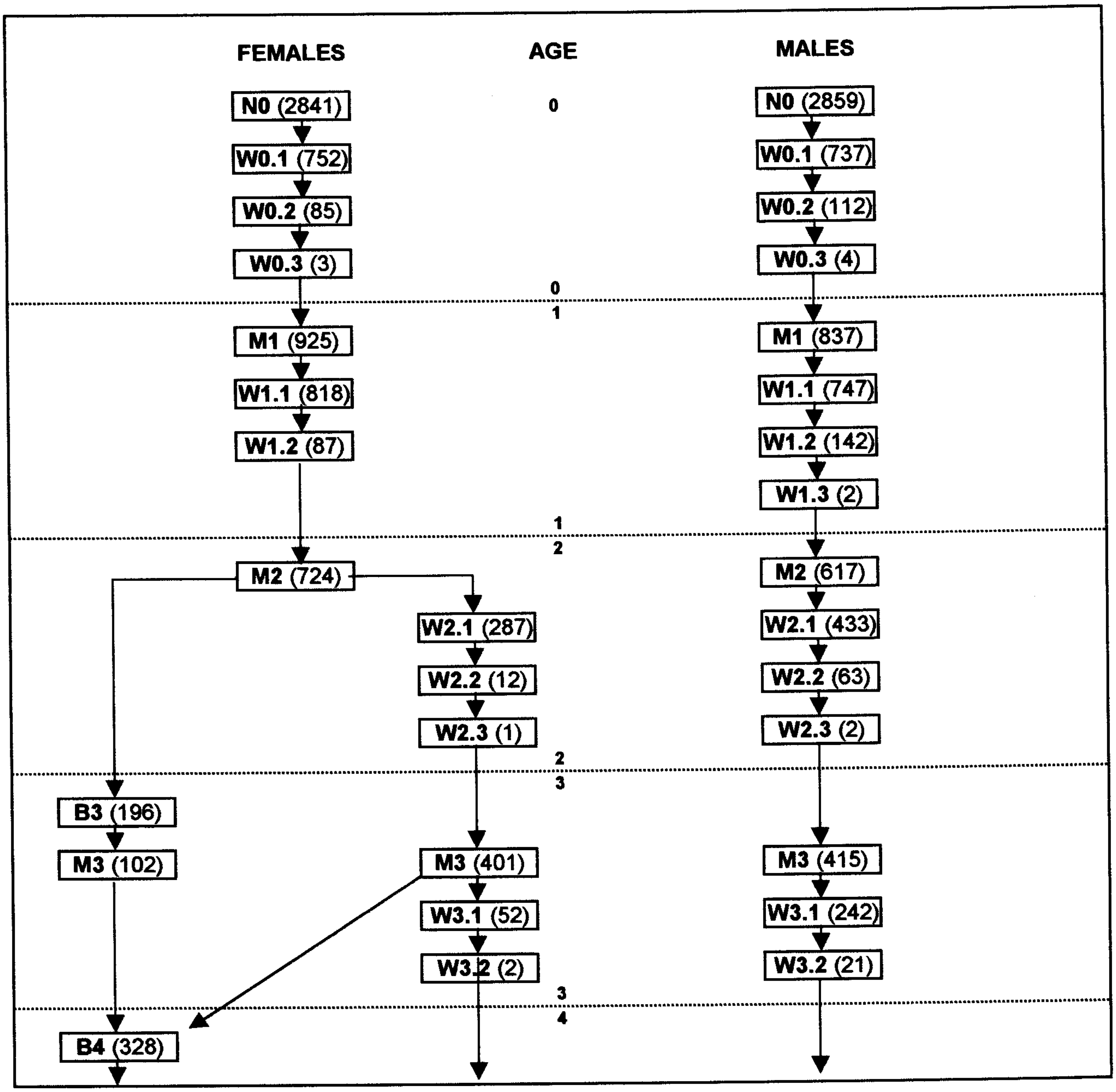
Movement		Norm.	Exp.	Gam.	Logn.	Chi-Sq.	Bin.	Pois.	Geom.
All dispersal	X^2	489	202	241	380	7037	22221	12803	251
	d.f	26	32	30	30	19	13	14	31
	p.	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01
Natal dispersal	X^2	251	94	107	184	2502	8142	4711	99
	d.f	26	27	27	26	17	12	13	27
	p.	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01
Breeding dispersal	X^2	229	129	148	189	1478	3513	2615	170
	d.f	20	22	20	20	15	10	11	22
	p.	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01
Moult dispersion	X^2	1531	162	322	696	40375	76237	76214	184
	d.f	32	41	38	40	25	15	18	40
	p.	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01
Winter dispersion	X^2	845	159	261	613	28540	60785	31686	154
	d.f	31	40	38	39	24	15	17	39
	p.	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01

Table A5.2 Fit of dispersal and dispersion data for male southern elephant seals, *Mirounga leonina*, at Marion Island to various standard distributions. Values are for X^2 tests. The following abbreviations are used for the various distributions: Norm. – normal, Exp. – exponential, Gam. – gamma, Logn. – log-normal, Chi-sq. – chi-squared, Bin. – binomial, Pois. – poisson, Geom. – geometric.

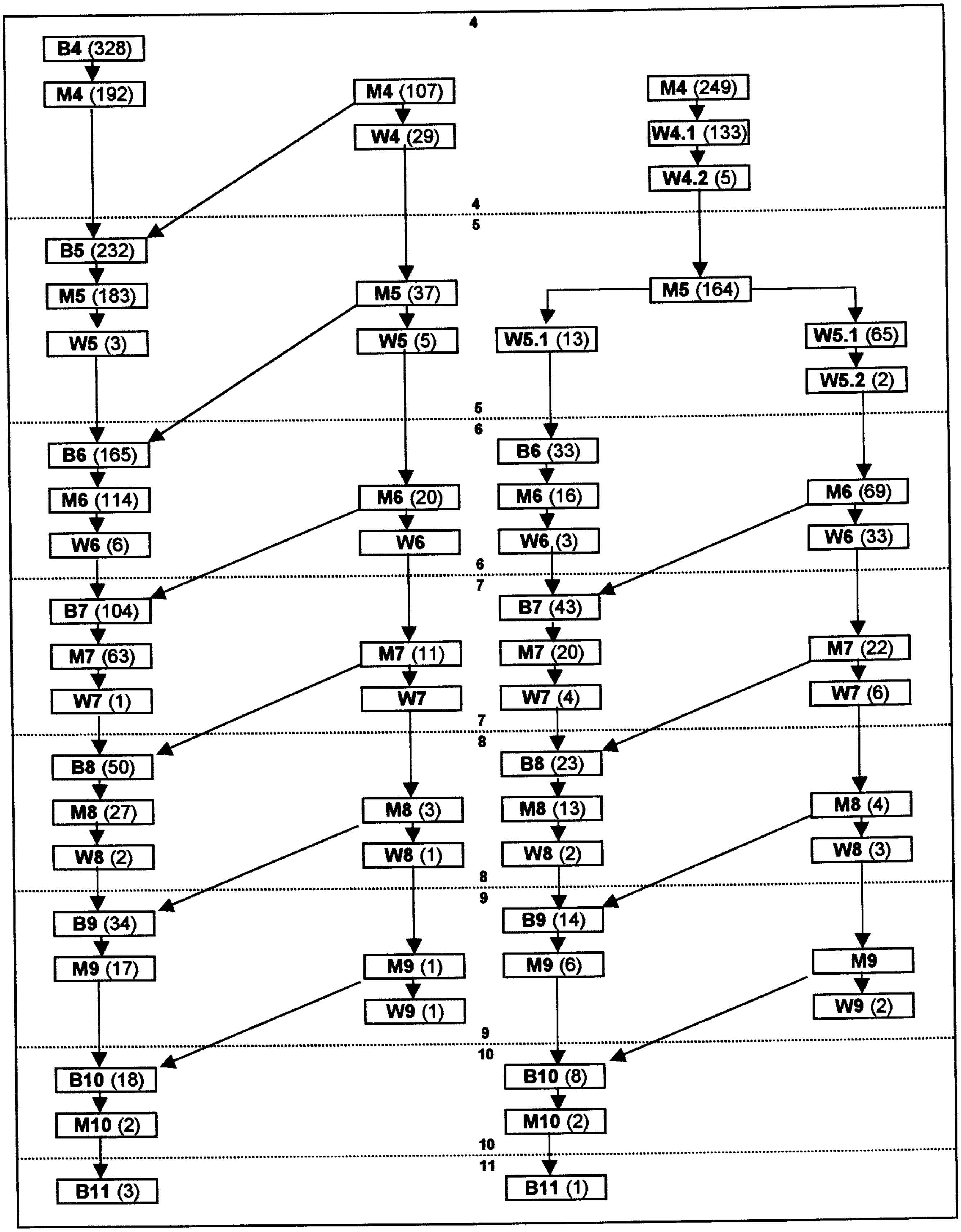
Movement		Norm.	Exp.	Gam.	Logn.	Chi-Sq.	Bin.	Pois.	Geom.
All dispersal	X^2	81	25	27	27	266	315	237	34
	d.f	13	12	10	10	10	7	7	11
	p.	<0,01	<0,05	<0,05	<0,01	<0,01	<0,01	<0,01	<0,01
Natal dispersal	X^2	52	12	14	17	98	227	159	19
	d.f	7	9	8	8	8	7	7	9
	p.	<0,01	**>0,05**	**>0,05**	<0,05	<0,01	<0,01	<0,01	<0,05
Breeding dispersal	X^2	17	4,7	9,4	8,4	10	16	12	12
	d.f	3	3	3	2	3	3	3	3
	p.	<0,01	**>0,05**	<0,05	<0,05	<0,05	<0,01	<0,01	<0,01
Moult dispersion	X^2	1024	144	295	629	23813	41645	48120	176
	d.f	30	39	36	38	23	14	17	38
	p.	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01
Winter dispersion	X^2	1310	145	667	31155	293	51253	54573	170
	d.f	31	40	40	24	38	14	17	39
	p.	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01	<0,01

APPENDIX 6

Figure A6.1 Recorded haulout events of male and female southern elephant seals, *Mirounga leonina*, on Marion Island. The first letter in the code below indicates the type of haulout: N - natal site, B - breeding haulout, M - moult haulout, and W - winter haulout. The second letter indicates the age of a seal at that haulout, and the third letter, the sequence number of haulouts, if there are more than one for a year. The numbers in parentheses indicate the number of seals tagged on Marion Island recorded hauling out for each haulout event, from November 1983 to November 1994.



Appendix 6 concluded



APPENDIX 7

Table A7.1 Probability matrix used to determine expected values of dispersal of southern elephant seals, *Mirounga leonina*, at Marion Island. Distances from a site are noted in the top row, while sites are noted in the left column. Other figures record the number of tagged and untagged seals hauling out to breed from 1990 - 1994, at each distance from each site. The bottom rows give the sum of the popularity of movement of any specific distance and the probability of movement of that distance.

Distance (km)	1	2	3	4	5	6	7	8	9	10	11
Site code											
MM046	2	0	0	0	0	11	6	0	846	55	712
MM051	11	6	839	62	712	62	476	336	844	68	629
MM052	6	857	55	712	487	376	675	180	68	629	16
MM053	846	61	723	536	327	853	68	629	2	16	76
MM054	901	718	60	814	673	180	68	629	18	73	35
MM055	774	899	482	347	844	68	629	0	89	5	32
MM056	827	483	1175	850	79	629	0	16	76	32	578
MM057	1248	391	851	907	635	11	16	76	32	576	6
MM058	863	1385	235	914	635	16	84	35	0	576	377
MM059	863	1565	123	1475	0	22	87	32	576	0	380
MM060	1476	240	780	691	855	79	35	11	576	377	3
MM061	1180	604	1341	55	23	915	38	587	6	374	792
MM062	1180	544	689	728	135	874	6	576	388	3	792
MM063	921	1005	487	728	131	878	576	6	391	792	0
MM064	877	673	392	563	744	631	846	380	798	11	0
MM065	697	196	749	408	1063	712	435	1638	0	6	47
MM066	89	632	100	1420	713	479	852	712	98	846	525
MM067	92	32	1205	74	1218	1128	476	60	803	14	1549
MM068	108	592	629	448	972	673	376	523	719	765	846
MM001	35	649	393	632	860	844	372	483	770	712	136
MM002	576	415	865	16	629	104	187	1383	376	561	968
MM003	380	1368	32	76	52	7	1339	142	853	583	916
MM004	380	1368	32	39	96	519	820	142	863	573	858
MM005	1172	576	0	71	80	726	629	142	436	1053	378
MM006	795	377	612	7	745	73	90	648	685	182	673
MM007	795	377	612	7	745	73	90	885	448	182	673
MM009	43	519	983	448	25	813	414	3	1085	1018	629
MM010	562	191	74	811	611	388	576	1028	1021	89	0
MM011	717	110	0	256	1172	376	978	1618	32	3	89
MM012	710	81	55	617	794	3	1373	1594	32	3	73
MM013	74	966	387	38	972	1042	792	380	0	576	32
MM014	256	454	193	1498	1078	0	0	792	374	6	576
MM015	636	76	0	1706	1025	36	0	786	9	377	576
MM016	619	19	1070	1209	519	7	36	0	792	3	377
MM017	382	1233	1037	74	191	526	36	0	0	792	374
MM018	2014	2	380	256	74	0	710	7	36	0	0
MM019	2014	2	380	237	19	74	191	526	36	0	340
MM020	2014	0	2	380	256	74	0	710	7	36	340
MM025	340	0	0	0	0	510	0	0	0	0	1042
MM026	510	0	0	0	0	340	0	0	0	0	0
Popularity	27985	19666	18022	20110	20189	15132	14382	17695	14185	11967	16445
Distance	1	2	3	4	5	6	7	8	9	10	11
Probability	0.0683	0.048	0.044	0.0491	0.0493	0.0369	0.0351	0.0432	0.0346	0.0292	0.0401

Appendix 7 continued

Distance (km)	12	13	14	15	16	17	18	19	20	21	22
Site code											
MM046	487	376	673	180	68	629	16	73	35	0	576
MM051	0	89	3	32	576	6	374	792	0	0	36
MM052	73	35	0	576	377	3	792	0	36	7	710
MM053	32	576	0	380	792	0	0	36	7	710	74
MM054	0	576	377	3	792	0	36	7	710	0	74
MM055	576	6	374	792	0	0	36	526	191	74	19
MM056	6	374	792	0	0	36	7	710	74	0	256
MM057	376	792	0	0	36	7	710	74	0	256	380
MM058	5	792	0	36	7	710	0	74	19	617	2
MM059	792	2	0	36	7	710	0	74	256	380	2
MM060	792	2	36	7	710	0	74	19	617	2	0
MM061	0	0	38	7	710	74	0	256	380	2	972
MM062	0	36	9	710	0	74	19	617	2	0	996
MM063	0	36	7	712	0	74	256	380	2	0	996
MM064	36	7	710	0	76	256	380	2	0	996	1018
MM065	7	710	0	74	256	382	2	0	996	1018	0
MM066	191	85	19	237	382	0	998	1018	0	0	0
MM067	80	11	256	380	2	972	1042	2	0	0	0
MM068	74	262	391	2	0	996	1018	0	2	0	0
MM001	858	623	2	11	996	1018	0	0	2	0	0
MM002	435	848	0	1002	1029	0	0	0	0	0	2
MM003	714	1027	1049	839	6	11	0	0	0	0	0
MM004	60	1708	1080	839	6	0	11	0	0	0	0
MM005	487	1708	1073	846	0	6	11	0	0	0	0
MM006	1372	1505	712	55	846	0	6	11	0	0	0
MM007	1372	1505	712	55	846	0	6	11	0	0	0
MM009	68	844	336	476	60	712	62	839	346	0	11
MM010	629	68	844	336	476	60	712	402	839	6	0
MM011	0	629	68	844	336	476	60	1107	7	839	6
MM012	16	629	68	844	336	476	400	712	62	839	6
MM013	76	16	0	629	68	1193	327	536	712	55	1356
MM014	32	3	89	0	969	68	844	336	476	570	767
MM015	0	35	73	356	629	68	180	673	886	487	712
MM016	576	0	375	73	16	629	68	1354	336	476	60
MM017	6	916	32	3	89	0	629	578	844	336	476
MM018	1132	380	0	576	32	586	16	0	629	68	853
MM019	792	374	6	576	542	3	89	0	629	68	844
MM020	0	792	380	0	1086	32	76	16	0	629	68
MM025	972	2	380	237	19	74	191	526	36	0	0
MM026	0	0	0	0	1018	996	0	382	237	19	74
Popularity	13124	18379	10964	12761	14196	11337	9448	12143	9368	8454	11346
Distance	12	13	14	15	16	17	18	19	20	21	22
Probability	0.032	0.0448	0.0268	0.0311	0.0346	0.0277	0.0231	0.0296	0.0229	0.0206	0.0277

Appendix 7 continued

Distance (km)	23	24	25	26	27	28	29	30	31	32	33
Site code											
MM046	377	3	792	0	36	7	710	0	74	19	617
MM051	526	191	74	19	237	380	2	972	1042	0	0
MM052	0	74	19	617	2	0	996	1018	0	0	0
MM053	0	256	380	2	972	1042	0	0	0	0	0
MM054	19	617	2	0	996	1018	0	0	0	0	0
MM055	237	380	2	972	1042	0	0	0	0	0	0
MM056	380	2	972	1042	0	0	0	0	0	0	0
MM057	2	972	1042	0	0	0	0	0	0	0	0
MM058	0	996	1018	0	0	0	0	0	0	0	0
MM059	0	996	1018	0	0	0	0	0	0	0	0
MM060	996	1018	0	0	0	0	0	0	0	0	0
MM061	1042	0	0	0	0	0	0	0	0	0	0
MM062	1018	0	0	0	0	0	0	0	0	0	340
MM063	1018	0	0	0	0	0	0	0	0	0	340
MM064	0	0	0	0	0	0	0	0	0	340	0
MM065	0	0	0	0	0	0	0	0	340	0	0
MM066	0	0	0	0	0	0	340	0	0	0	0
MM067	0	0	0	0	0	0	340	0	0	0	0
MM068	0	0	0	0	0	340	0	0	0	0	510
MM001	0	0	0	0	340	0	0	0	0	510	0
MM002	0	0	0	340	0	0	0	0	510	0	0
MM003	2	0	340	0	0	0	0	510	0	0	0
MM004	2	340	0	0	0	0	510	0	0	0	0
MM005	0	342	0	0	0	0	510	0	0	0	0
MM006	340	0	2	0	0	510	0	0	0	0	0
MM007	340	0	2	0	0	510	0	0	0	0	0
MM009	0	0	510	0	2	0	0	0	0	0	0
MM010	11	510	0	0	0	2	0	0	0	0	0
MM011	11	510	0	0	0	0	2	0	0	0	0
MM012	510	11	0	0	0	0	2	0	0	0	0
MM013	0	6	11	0	0	0	0	0	2	0	0
MM014	7	839	6	11	0	0	0	0	0	2	0
MM015	55	846	0	6	11	0	0	0	0	0	2
MM016	712	62	839	6	0	11	0	0	0	0	2
MM017	60	712	62	839	6	0	11	0	0	0	0
MM018	327	536	712	55	846	0	6	11	0	0	0
MM019	336	476	60	712	62	839	6	0	11	0	0
MM020	853	327	536	712	55	846	0	6	11	0	0
MM025	792	374	6	576	32	3	89	0	629	68	844
MM026	191	519	7	36	0	792	3	377	576	32	3
Popularity	10164	11915	8412	5945	4639	6300	3527	2894	3195	971	2658
Distance	23	24	25	26	27	28	29	30	31	32	33
Probability	0.0248	0.0291	0.0205	0.0145	0.0113	0.0154	0.0086	0.0071	0.0078	0.0024	0.0065

Appendix 7 concluded

Distance (km)	34	35	36	37	38	39	40	41	42	43	43.5
Site code											
MM046	2	510	996	1018	0	0	340	0	0	0	0
MM051	0	0	0	0	0	0	0	510	340	0	0
MM052	0	0	0	0	0	0	340	0	510	0	0
MM053	0	0	0	0	0	340	0	0	0	0	510
MM054	0	0	0	0	340	0	0	0	0	510	0
MM055	0	0	0	0	340	0	0	0	0	510	0
MM056	0	0	0	340	0	0	0	0	510	0	0
MM057	0	0	340	0	0	0	0	510	0	0	0
MM058	0	340	0	0	0	0	0	510	0	0	0
MM059	0	340	0	0	0	0	510	0	0	0	0
MM060	340	0	0	0	0	510	0	0	0	0	0
MM061	340	0	0	0	0	510	0	0	0	0	0
MM062	0	0	0	0	510	0	0	0	0	0	0
MM063	0	0	0	0	510	0	0	0	0	0	0
MM064	0	0	0	510	0	0	0	0	0	0	0
MM065	0	510	0	0	0	0	0	0	0	0	0
MM066	510	0	0	0	0	0	0	0	0	0	0
MM067	510	0	0	0	0	0	0	0	0	0	0
MM068	0	0	0	0	0	0	0	0	0	0	0
MM001	0	0	0	0	0	0	0	0	0	0	0
MM002	0	0	0	0	0	0	0	0	0	0	0
MM003	0	0	0	0	0	0	0	0	0	0	0
MM004	0	0	0	0	0	0	0	0	0	0	0
MM005	0	0	0	0	0	0	0	0	0	0	0
MM006	0	0	0	0	0	0	0	0	0	0	0
MM007	0	0	0	0	0	0	0	0	0	0	0
MM009	0	0	0	0	0	0	0	0	0	0	0
MM010	0	0	0	0	0	0	0	0	0	0	0
MM011	0	0	0	0	0	0	0	0	0	0	0
MM012	0	0	0	0	0	0	0	0	0	0	0
MM013	0	0	0	0	0	0	0	0	0	0	0
MM014	0	0	0	0	0	0	0	0	0	0	0
MM015	0	0	0	0	0	0	0	0	0	0	0
MM016	0	0	0	0	0	0	0	0	0	0	0
MM017	2	0	0	0	0	0	0	0	0	0	0
MM018	0	0	2	0	0	0	0	0	0	0	0
MM019	0	0	0	2	0	0	0	0	0	0	0
MM020	0	0	0	2	0	0	0	0	0	0	0
MM025	336	476	60	712	62	839	8	0	11	0	0
MM026	73	18	629	68	844	336	476	71	718	62	839
Popularity	2113	2194	2027	2652	2606	2535	1674	1601	2089	1082	1349
Distance	34	35	36	37	38	39	40	41	42	43	44
Probability	0.0052	0.0054	0.0049	0.0065	0.0064	0.0062	0.0041	0.0039	0.0051	0.0026	0.0033