INDIVIDUAL HISTORY OF MOVEMENT AND THE DISPERSAL OF SOUTHERN ELEPHANT SEALS

by

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Declaration:

I, Gordon John Gregory Hofmeyr, declare that the thesis, which I hereby submit for the degree of Ph.D. (Zoology) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature………………………

Date……………………………

2013

University of Pretoria

South Africa

Southern elephant seals at King Penguin Bay, Marion Island. Photo – G. Hofmeyr

“ ‘He comes out, into the wave-worn caves, and lies him down to rest: while drove upon drove of his seals, bred from the saltwater by an ocean-nymph, forsake the grey brine and sleep too around him, bitter-scenting the place because their breathing holds the bitterness of the salt abysses of the sea.’ ”

Homer – The Odyssey

Individual history of movement and the dispersal of southern elephant seals

by

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Supervisor: Prof. M.N. Bester

Department: Zoology and Entomology

Degree: Doctor of Philosophy (Zoology)

ABSTRACT

While studies of dispersal note significant fidelity to natal site and to the site of first reproduction, few consider fidelity to other sites, and none have done so systematically. This study examined fidelity to all terrestrial sites within the study area during the course of its life, by a migratory marine predator, the southern elephant seal, *Mirounga leonina*. It also attempted to assess the role played by the winter haulout in terms of site fidelity. Finally it examined the influence of possible deterioration in spatial memory over time on site fidelity. The data used in this study were generated by a long-term mark-recapture programme conducted at subantarctic Marion Island.

Although immature elephant seals of both sexes return to the vicinity of their natal sites, they appear to avoid popular breeding beaches, returning closest to the site previously used. At the first reproductive haulout, however, females return closer to their natal site than any other site, while males, although hauling out in the vicinity of their natal site, haul out closest to sites used in the year prior to the first breeding haulout. Subsequently, adults of both sexes breed closest to the breeding haulout of the previous year and moult closest to the moult haulout of the previous year. While males show greater site fidelity during the breeding season, there is no difference in site fidelity during the moult. Primiparous females show greater levels of site fidelity if recorded in the study site as an immature animal during either the winter or the moult haulouts. Also in female elephant seals, lower site fidelity is associated with an increase in the duration of period of absence from a site, and a lower number of visits to a site.

Various factors related to site familiarity, social factors and anthropogenic disturbance may be responsible for the lack of strict site fidelity that is evident. Dispersal patterns may differ between the sexes due to differences in their life history. While purpose of the winter haulout by immature seals may be to increase familiarity with haulout sites, and thus site fidelity, the moult haulout also plays a role.

Keywords: dispersal, site fidelity, philopatry, movement, habitat selection, spatial memory, southern elephant seals, *Mirounga leonina*, Subantarctic

FOREWORD

This study examines dispersal and site fidelity of southern elephant seals and attempts to assess what periods, if any, of the seals history of terrestrial site use influence their later site selection. It consists of six chapters. **Chapter 1** introduces the study of dispersal, the study animal and the study area. It then summarises the current state of knowledge of dispersal in pinnipeds concentrating on those species in which it has most been examined. This is followed by the questions that I have attempted to answer. Finally, it addresses the necessary assumptions made in completing the thesis. Chapters 2 – 5 provide the main course and each is presented as a complete paper. **Chapter 2** examines the dispersal of female elephant seals in relation to their history of terrestrial site use within the study area. **Chapter 3** does the same for male seals, and compares the results to those of females. **Chapter 4** looks at the winter haulout period, attempting to assess its purpose in light patterns of dispersal shown. And **Chapter 5** attempts to assess patterns of dispersal and site fidelity in relation to the cognitive abilities of the seals, especially in terms of memory. **Chapter 6** attempts to draw a conclusion from results and proposes further avenues of research. All terms specific to this field of study or this thesis are defined when first used. These definitions are repeated in a glossary in the **appendices**. Other appendices give examples of haulout records of female and male elephant seals, list the haulout sites at Marion Island, list all possible haulout events, and the numbers of animals participating in them, and finally repeat an early description of elephant seals. This study is condensed in a brief **abstract** at the beginning and a longer, point-form **summary** at the end.

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This thesis is based on twenty years worth of data, the collection of which often took place under conditions often made arduous by the nature of the study site, the prevailing climate and the normal behaviour of the study animals. I only contributed to three years worth of these data. Those who participated in the collection of these data are to be counted as true Islanders: Marthán Bester, Craig Saunders, Steve Atkinson, Pete Bartlett, Anton Hunt, Ian Wilkinson, Charlie Pascoe, Jaco Swart, Rory Heather-Clarke, Sam Ferreira, Hendrik Pansegrouw, Francois Roux, Jo Fourie, Jay de Lange, André la Cock, Johannes Kloppers, Frans Jonker, Steve Kirkman, Pierre Pistorius, Derrick Shingwenyana, Mike de Maine, Tenda Mathagu, Bianca Harck, Newi Makhado, Tambu

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Chapter 1 ▪ Introduction

Southern elephant seal breeding aggregation, Archway Bay, Marion Island. Photo – G. Hofmeyr

CHAPTER 1

INTRODUCTION

Dispersal and the history of movement

Site selection

One of the most important behaviours shown by an animal, in terms of its survival and reproductive success, is the selection or attempted selection of the site or sites that it will occupy during the various stages of its life (Caughley 1977; Manley *et al.* 1993). Accessibility to sites varies among species; many animals have a relatively limited ability to select sites and must rely on chance to place them and their offspring or propagules in a favourable habitat (Matthiopoulos 2003). Other animals, however, have remarkable abilities of movement. This group includes some of the larger vertebrates. Furthermore, some animals among this group are able to travel relatively efficiently for long periods and through media that provide few barriers (Schmidt-Nielsen 1972; Boyd 2002; Gleiss *et al.* 2011). Notable examples here are some species of birds and some species of marine vertebrates, such as various fish, turtles, cetaceans and pinnipeds (Boyd 2002; Gleiss *et al.* 2011). These animals frequently undertake long migrations between distant sites during the course of their lives. These animals are potentially able to move among a variety of habitats and to select those suitable or most suitable (Dingle 1996; Clobert *et al.* 2001). The ability to move among habitats is beneficial, because (1) animals change during the course of their lives, with concurrent changes in resource requirements, and (2) accessible environments change, with concurrent changes in the types and levels of resources available. The selection of a site will depend on a number of factors (Figure 1.1). Among these are the accessibility of that site, the knowledge of its existence, location, and characteristics, and an ability to assess the characteristics of newly encountered sites (Greenwood & Harvey 1982; Manley *et al.* 1993; Matthiopoulos 2003). Therefore, in addition to an ability to move among sites, in order to survive in its environment, an animal will need to be able to assess the quality of a site, remember the quality of that site, remember the features of the site that will enable it to exploit resources at that site efficiently, and remember features in the vicinity of that site that will aid in locating that site. During the course of its existence an animal may have built up a body of knowledge of previously visited sites that could aid it in the selection of a site. This knowledge may be modified by information gained concerning the current state of a site in terms of resources and perceived dangers, and the social environment present (Greenwood & Harvey 1982; Manley *et al.* 1993).

Definitions

The term *dispersal* has been used in a variety of ways (see Baker 1978; Dingle 1996; Clobert *et al.* 2001). I follow a common biological usage (for example Howard 1960; Greenwood 1980; Shields 1987) in defining it as the movement of individual animals from one location to another, where reproduction is attempted. Reproduction, in this case, being either mating or parturition. *Natal dispersal* is movement in relation to the natal site, whereas *breeding dispersal* is movement in relation to a site used for reproduction. Another important definition is *philopatry*, which is defined as a return by an animal to its natal site to reproduce. A more broadly defined term is *site fidelity*, which is the return of an animal to any previously used site for any purpose. These

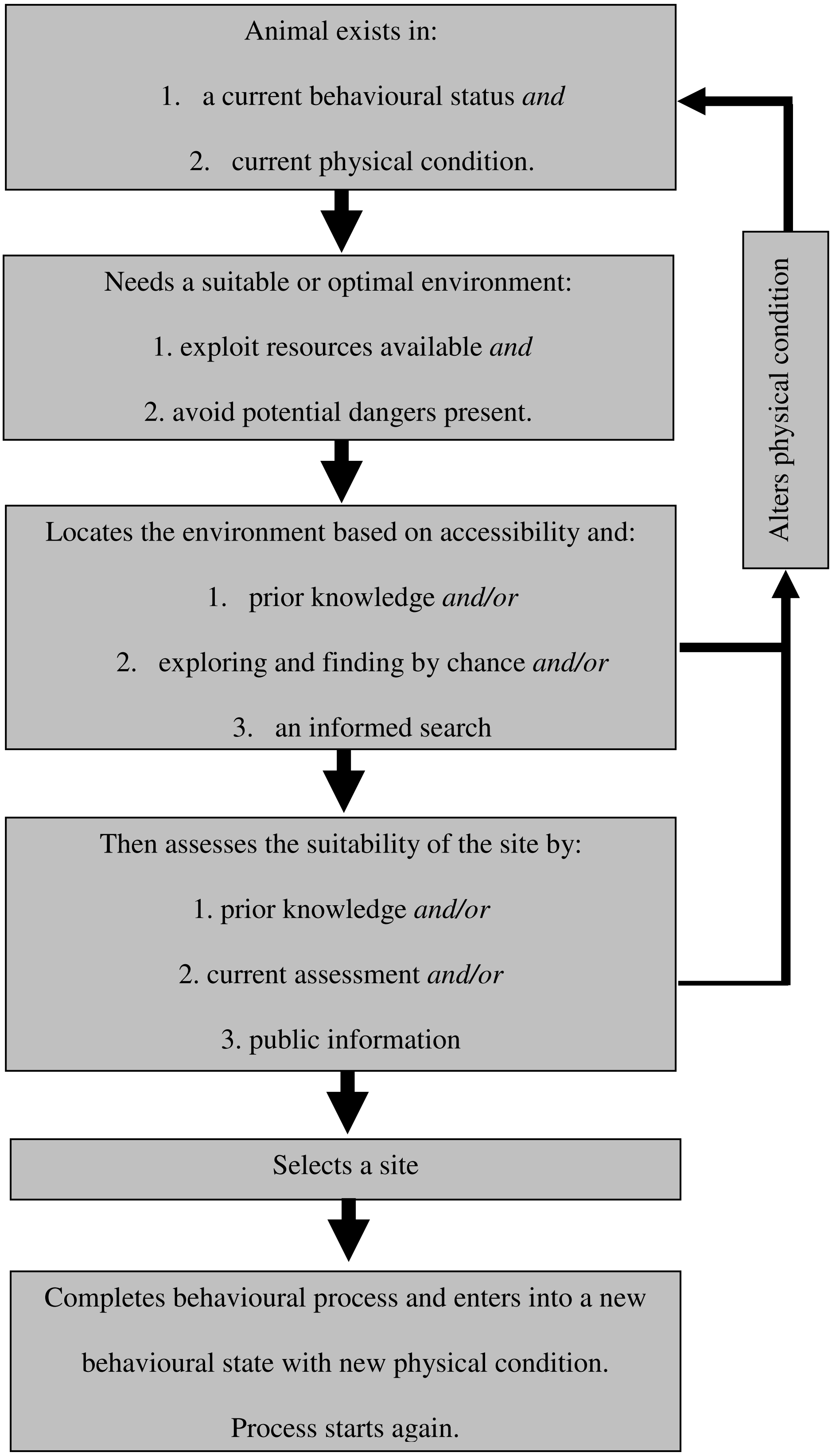

Figure 1.1 Schematic diagram showing postulated factors associated with site selection by an animal.

definitions broadly follow Howard (1960), Greenwood (1980) and Shields (1987). Finally, *history of movement* describes the record of the interseasonal movements of an animal that result in a pattern of displacements between seasonally used sites over the course of its life. History of movement does not refer to finer scale movements of animals on a day-to-day basis, or even within a season (for example Munyai 2006).

Consequences of site fidelity and dispersal

The fidelity of individual animals to a particular site or population and their dispersal to other sites or populations is important for a number of reasons, and on a number of levels. Firstly, it affects the distribution and size of populations through the colonisation of potential habitat and the rescue of small unviable populations (Matthiopoulos *et al.* 2005). Secondly, levels of dispersal lead to the movement of genetic material and thus influence the establishment of population genetic structure (Caughley 1977; Gaines & McClenaghan 1980; Lidicker & Caldwell 1982; Matthiopoulos *et al.* 2005). Thirdly, dispersal may influence individual survival through the levels of resource availability at a particular site and the disease, injury and mortality risks of a particular site (Caughley 1977; Gaines & McClenaghan 1980; Moore & Ali 1984). Finally, it may influence the reproductive success of individuals through the availability of potential mates and resources, and the risks of mortality faced by offspring and the potential resources available to those offspring (Caughley 1977; Beletsky & Orians 1991; Pärt 1994).

Patterns of dispersal

Patterns of dispersal shown by animals vary among species, and within species among populations, and among age and sex classes (Greenwood 1980; Dobson 1982; Pärt

1991). These patterns of dispersal have been related to life history characteristics and to characteristics of the environment, including resource availability and distribution (Greenwood 1980; Dobson 1982). Immature animals typically disperse farther than adults for a number of possible reasons: 1. their lack of familiarity with their environment, 2. a need to assess their environment through exploration, and 3. they may be unable to compete with older animals (Greenwood 1980; Greenwood & Harvey 1982). Adult animals frequently show an increase in site fidelity as they age (Greenwood & Harvey 1982; Pärt 1995).

Patterns of sex bias in dispersal have been related to social structure and life history adaptations to the environment (Greenwood 1980; Dobson 1982; Greenwood & Harvey 1982). It has been noted that females are the predominant dispersing sex in monogamous species, or species showing resource defence polygyny, whereas males are the predominant dispersers in species showing mate defence polygyny. Accepted theory in explanation is that, where males defend resources to which females are attracted, males gain the most from philopatry since familiarity with an area would favour their chances of obtaining and keeping a territory. Females therefore disperse to avoid the deleterious effects of inbreeding. Conversely, in systems where males defend access to mates and associated reproductive opportunities, dispersal would be male biased as their reproductive success would not be linked to knowledge of an area. However, females would invest more in protecting resources, which would require a better knowledge of an area (Greenwood 1980; Dobson 1982; Greenwood & Harvey 1982).

Most studies of dispersal, however, have concentrated on animals that are largely sedentary. However, the problems facing migratory animals, in terms of the selection of suitable breeding sites or home ranges, are very different. While non-migratory animals expend energy and time in attempting to find suitable habitat when moving away from their natal site, and therefore face the costs of dispersal, migratory animals incur costs in attempting to return to a previously used suitable site (Morton 1992; Pärt 1995). In this regard Pärt (1995) stated that the accuracy with which a migratory animal returns to a previously used site is a compromise between the benefits attained from the use of that site, and the costs in energy and time spent finding and returning to it.

The study animal – southern elephant seals

Two species of elephant seals are extant; the southern elephant seal, *Mirounga leonina*, which is the subject of this study, and the closely related northern elephant seal, *M. angustirostris* (King 1983). Both undergo an annual double migration between foraging grounds and isolated haulout sites, at which they are born, breed and moult (Bartholomew & Hubbs 1960; Carrick *et al.* 1962b; Hindell & Burton 1988; Wilkinson 1992; Stewart *et al.* 1994). The mating system is polygynous, with mate-defence rather than territorial-defence. Breeding seasons are highly synchronised. (Laws 1956; Carrick *et al.* 1962b; McCann 1981; Bonner 1989; Wilkinson & van Aarde 1999). Speciation is thought to have occurred approximately one million years ago (Hoelzel *et al.* 1993). Despite this the two species share many similarities in appearance and behaviour. They differ primarily in their range and in the timing of their terrestrial periods ashore (Bonner 1989; Ling & Bryden 1992). Northern elephant seals forage in the north-west Pacific ocean (DeLong *et al.* 1992; Stewart & DeLong 1992), and come ashore to breed in the boreal late winter and to moult in the boreal spring and early summer on islands and a few mainland sites along the coast of California and Baja California (Bartholomew & Hubbs 1960; Stewart *et al.* 1994). Southern elephant seals haul out on islands of the Southern Ocean. They breed in the austral spring and moult in the austral summer (Laws 1954).

Description

The southern elephant seal is the largest species of pinniped; with adult males reaching masses of two to four tons and lengths of up to 4.5 metres. This species shows considerable sexual dimorphism, with adult females being considerably smaller and only reaching masses of 400 to 900 kilograms and lengths of up to 2.8 metres (Figure 1.2). Newborn pups weigh between 40 and 46 kilograms but reach masses of 100 to 160 kilograms by weaning three weeks later (Figure 1.3) (Laws 1993). Females first haul out to pup at ages of three to six years, and males typically breed for the first time at seven to ten years of age (Laws 1956; Carrick *et al.* 1962a; Jones 1981; McCann 1981). At the study site, however, the onset of breeding is typically younger in males, from six to eight years (Bester & Wilkinson 1994; Pistorius *et al.* 2001; Kirkman *et al.* 2004).

Life history

Southern elephant seals are predominantly marine. Adult females spending some 85 % of each year at sea while adult males spend between 70 and 85 % (Carrick *et al.* 1962a; Hindell & Burton 1988; Wilkinson 1992; McIntyre *et al.* 2010). Their foraging grounds may be located over 3 000 kilometres from terrestrial haulout sites

Figure 1.2 Adult male southern elephant seals *Mirounga leonina* with adult females on Marion Island. Photo: G. Hofmeyr

Figure 1.3 Adult female southern elephant seals *Mirounga leonina* on Marion Island suckling a neonate with a weaned pup lying in the foreground. Photo: G. Hofmeyr

(Bester & Pansegrouw 1992; Jonker & Bester 1998). Four types of terrestrial periods are experienced over the course of their lives: the breeding, moult and winter haulouts, and the natal terrestrial period.

The breeding haulout is highly synchronized and takes place from late August to late November. Adult females spend approximately a month ashore during the breeding season, while adult males may spend one to three months ashore. During this time adult females will haul out in large aggregations known as "harems" (Carrick *et al.* 1962a; Bonner 1989). While these may contain as many as a thousand females (Bonner 1989) those at the study site (Figure 1.4), and for the duration of the study, seldom contained more than 40 adult females (Wilkinson 1992, MRI unpublished data). Some two to three days after females come ashore they give birth to a single pup, which they will suckle for some three weeks. Mating takes place shortly before the pup is weaned and the adult female returns to the sea a few days later. Breeding aggregations are ephemeral, and do not last beyond the breeding season. Access to all females in one breeding aggregation is defended by a dominant adult male, who is known as a "beachmaster". Where harems are large enough, the dominant adult male is unable to prevent other adult males from gaining access to portions of the harem, and mating with cows. These sub-dominant males are known as "assistant-beachmasters". Also associated with breeding aggregations are subordinate males, known as "bachelors". These usually lie close to harems, and occasionally attempting to mate with females arriving at or leaving the beach. Where bachelors attempt to take over control of a harem they are known as "challengers" (Laws 1956; Carrick *et al.* 1962a; McCann 1981; Wilkinson & van Aarde 1999). Both assistant-beachmasters and challengers were

Figure 1.4 A breeding aggregation of southern elephant seals *Mirounga leonina* among king penguins *Aptenodytes patagonicus* at Funk Bay, Marion Island. Associated with many of the adult females are their small, dark pups. The arrow on the left indicates the beachmaster, while the arrow on the right indicates a bachelor male. Photo: G. Hofmeyr

Figure 1.5 An aggregation of moulting southern elephant seals *Mirounga leonina* on Marion Island. Photo: G. Hofmeyr

recorded very seldom during the study (Wilkinson 1992, MRI unpublished data).

While only adult seals participate in the breeding haulout, animals of all age classes must haul out once a year to moult (Figure 1.5). This takes place from November to March. Adult seals usually spend two months at sea between the breeding and moulting season, and one month ashore during the moult. The third period ashore is the winter haulout. This takes place from mid-January to mid-September, with the majority of haulouts between March and August (Kirkman 1999; Kirkman *et al.* 2001a). Each haulout may last for a few days to several weeks. The great majority of animals ashore during this period are immatures, but a small number of adults also take part (Kirkman *et al.* 2001a).

In addition to the three types of haulouts, elephant seals spend a fourth period ashore, which is known as the natal period. This includes both the three weeks new born pups spend suckling and gaining weight, and a period of 4-6 weeks after weaning during which time they lie in groups known as “weaner pods” (Lenglart & Bester 1982; Wilkinson & Bester 1990).

Elephant seals therefore have a regular pattern of lifetime haulouts, separated by long periods spent foraging at sea: as a pup they will spend a few weeks ashore after birth and weaning. As an immature they will alternate between an annual moult and winter haulouts. While not all immatures haul out every winter, approximately 10 % undertake two winter haulouts in a year, and some even undertake a third winter haulout. As adults elephant seals alternate between breeding and a moult haulouts. Many adult females skip breeding haulouts at Marion Island (de Bruyn *et al.* 2011) and a very small number will come ashore during the winter (Mammal Research Institute unpublished data).

Distribution

While most haulout sites for southern elephant seals are on Subantarctic and Antarctic islands (Figure 1.6), a number haul out regularly at sites on the coasts of South America (Campagna & Lewis 1992) and Antarctica (Murray 1981; Bester 1988). They forage at sea between about 40°S and the Antarctic Continent. Occasional vagrants have been recorded on the coasts of Southern Africa (Oosthuizen *et al.* 1988), Tasmania and New Zealand (Taylor & Taylor 1989).

The global population of southern elephant seals is estimated at 750 000 individuals (McCann 1985; SCAR-EGS 2011). Four metapopulations or stocks are extant (Table 1.1). A further four populations have become extinct in historical times, each of which was possibly a separate metapopulation: St. Helena Island, Tristan da Cunha, Islas Juan Fernández and the Bass Straits (Carrick & Ingham 1962a; Wace & Holdgate 1976; Bester 1980). Stoddart (1972) also provides evidence that southern elephant seals regularly visited islands of the temperate Indian Ocean during historical times, though it is unknown where such animals would have originated. Relatively little movement of individuals takes place between extant metapopulations and consequently there is a degree of genetic isolation among them (Gales *et al.* 1989; Hoelzel *et al.* 1993). Further hierarchical population structuring may occur (Table 1.2) with stocks being separated into archipelagos, individual islands, isolated beaches and breeding aggregations. For example, the Kerguelen stock includes four archipelagos (Îles Kerguelen, Heard and

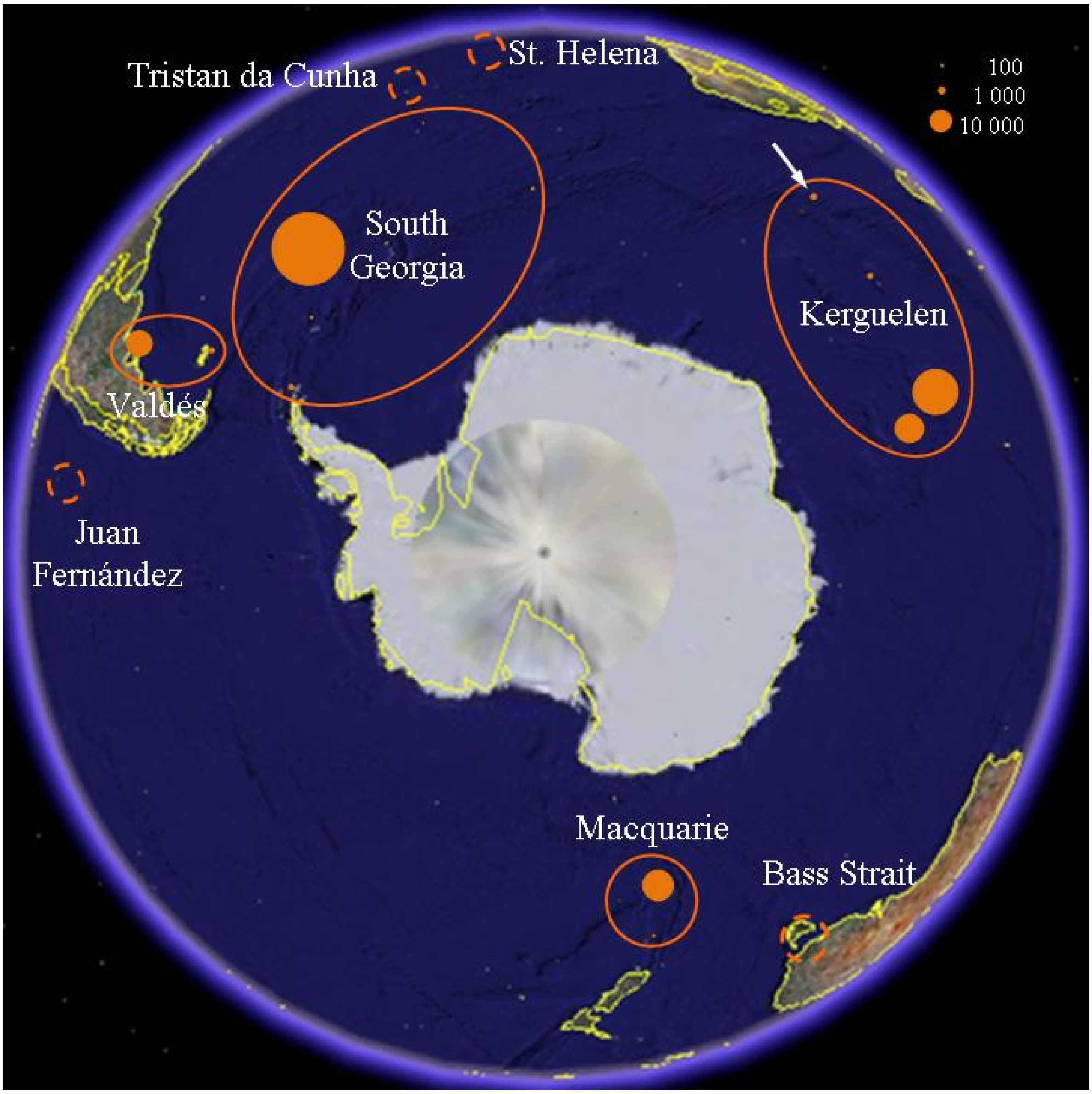

Figure 1.6 Distribution of southern elephant seal *Mirounga leonina* breeding haulouts. The closed orange circles indicate relative pup production at each island or island group. The orange lines enclose islands that form part of a metapopulation or stock. Solid lines enclose extant metapopulations, while dotted lines enclose populations that have become extinct in historical times. The arrow indicates the location of the study site.

Table 1.1 Estimated pup production of island populations of southern elephant seals, *Mirounga leonina*. Data adapted from SCAR EGS (2011)

Meta-population	Island/Island group	Estimated pup production	Year of estimate	Trends in abundance	Period	Reference
South Georgia	South Georgia Is.	113 444	1995	Stable	1985-1995	Boyd *et al.* 1996
	South Orkney Is.	< 100	1985	Uncertain		McCann 1985
	Bouvetøya	89	1998	Uncertain		Kirkman *et al.* 2001b
	Gough Is.	18	1998	Declining	1975-1998	Bester *et al.* 2001
	King George Is. (S. Shetland Is.)	290-400	2003	Fluctuating	1999-2003	Carlini (pers. comm.) in SCAR-EGS 2011
	Duthoit Point, Nelson Is. (S. Shetland Is.)	50-135	2003	Fluctuating		Carlini (pers.comm.) in SCAR-EGS 2011
	Cape Shireff, Livingston Island (S. Shetland Is.)	3-84	2003	Fluctuating	1998-2005	Goebel (pers. comm.) in SCAR-EGS 2011
Peninsula Valdés	Peninsula Valdés	14 510	2001	Increasing	1982-2001	Lewis (pers. comm.) in SCAR-EGS 2011
	Falkland Is.	Approx. 1000	1960	Uncertain		Laws 1960
	Sea Lion Is. (Falklands)	532	2007	Stable	1989-2007	Galimberti (pers.comm.) in SCAR-EGS 2011

Table 1.1 (completed) Estimated pup production of island populations of southern elephant seals, *Mirounga leonina*. Data adapted from SCAR EGS (2011).

Meta-population	Island/Island group	Estimated pup production	Year of estimates	Trends in abundance	Period	Reference
Kerguelen	Marion Is.	516	2007	Increasing?	2005-2007	McMahon *et al.* 2009
	Prince Edward Is.	130	2004	Declined	1977-2004	Bester & Hofmeyr 2005
	Heard Is.	17 000 – 18 000	1992	Increasing?	1982-1992	Slip & Burton 1999
	Courbet Peninsula (Îles Kerguelen)	>40 000	2009	Stable	1987-2009	Guinet *et al.* 1999, Authier *et al.* 2011(Authier *et al.* 2011)
	Île de la Possession (Îles Crozet)	570	1997	Stable	1990-1997	Guinet *et al.* 1999
Macquarie	Macquarie Is.	20 374	2004	Stable to increasing	1997-2004	Van den Hoff *et al.* 2007
	Campbell Is.	5	1986	Declining	1947-1986	Taylor & Taylor 1989
	Antipodes Is.	113	1978	Uncertain		Taylor & Taylor 1989

Table 1.2 Putative hierarchical population structure of southern elephant seals, *Mirounga leonina*.

Population unit		Example
Global Population	----------------	southern elephant seals
Metapopulation (or stock)	------------	South Indian Ocean
Archipelago	--------	Prince Edward Islands
Island	------	Marion Island
Beach (or site)	----	Goney Bay
Breeding aggregation (or harem)	--	Goney Bay West
Individual	-	RR 632 ♀

McDonald Islands, Îles Crozet and the Prince Edward Islands), which are all separated by distances of several hundred or thousand kilometres. Some degree of movement takes place within this stock (Bester 1989; Oosthuizen *et al.* 2011). While the Prince Edward Islands Archipelago (PEIA) contains two islands, only separated by 19 kilometres, the distances separating the islands of other archipelagos may be up to 100 kilometres (Guinet *et al.* 1992). Marion Island, within the PEIA, has some 40 beaches on which elephant seals regularly haul out and some 25 on which they regularly breed. These beaches are separated by distances of up to 5 kilometres from their nearest neighbours. The larger beaches may support more than one breeding aggregation, which may be separated from one another by distances of up to 100 metres.

Study site

Location

The Prince Edward Island Archipelago consists of two islands: Prince Edward Island itself and the study site, Marion Island (Figure 1.7). This remote archipelago (46°54' S, 37°45' E) is located in the subantarctic zone of the Southern Ocean, some 2 180 kilometres south of southern Africa and 2 300 kilometres north of Antarctica (Figure 1.6). The nearest other islands are the isolated Îles Crozet, some 950 kilometres to the East (PEIMPWG 1996). The two islands of the archipelago are separated by 19 kilometres and are therefore similar in topography and climate, and support similar indigenous biota (Verwoerd 1971; Gremmen 1981; Smith 1987). Differences in their history, especially over the last 50 years, are responsible for Marion Island supporting a far larger number of exotic species (Gremmen 1981; Smith 1987). Marion Island is also the larger of the two islands with an area of 290 kilometres^2 and a circumference of approximately 87 kilometres, while Prince Edward Island has an area of only 45 kilometres^2 (PEIMPWG 1996).

Topography

The islands are of volcanic origin and are considered to be some 500 000 years old. Two periods of volcanic activity and a dividing glacial period are responsible for the islands topography. Marion Island rises from a vegetated coastal plane to a rough mountainous interior, with the highest peak reaching 1 230 metres (Verwoerd 1971). The coastline is irregular but only indented by a few small bays. Cliffs of between 15 and several hundred metres in height form the majority of the coastline. These are broken in a number of places by beaches, especially where rivers flow out to the sea.

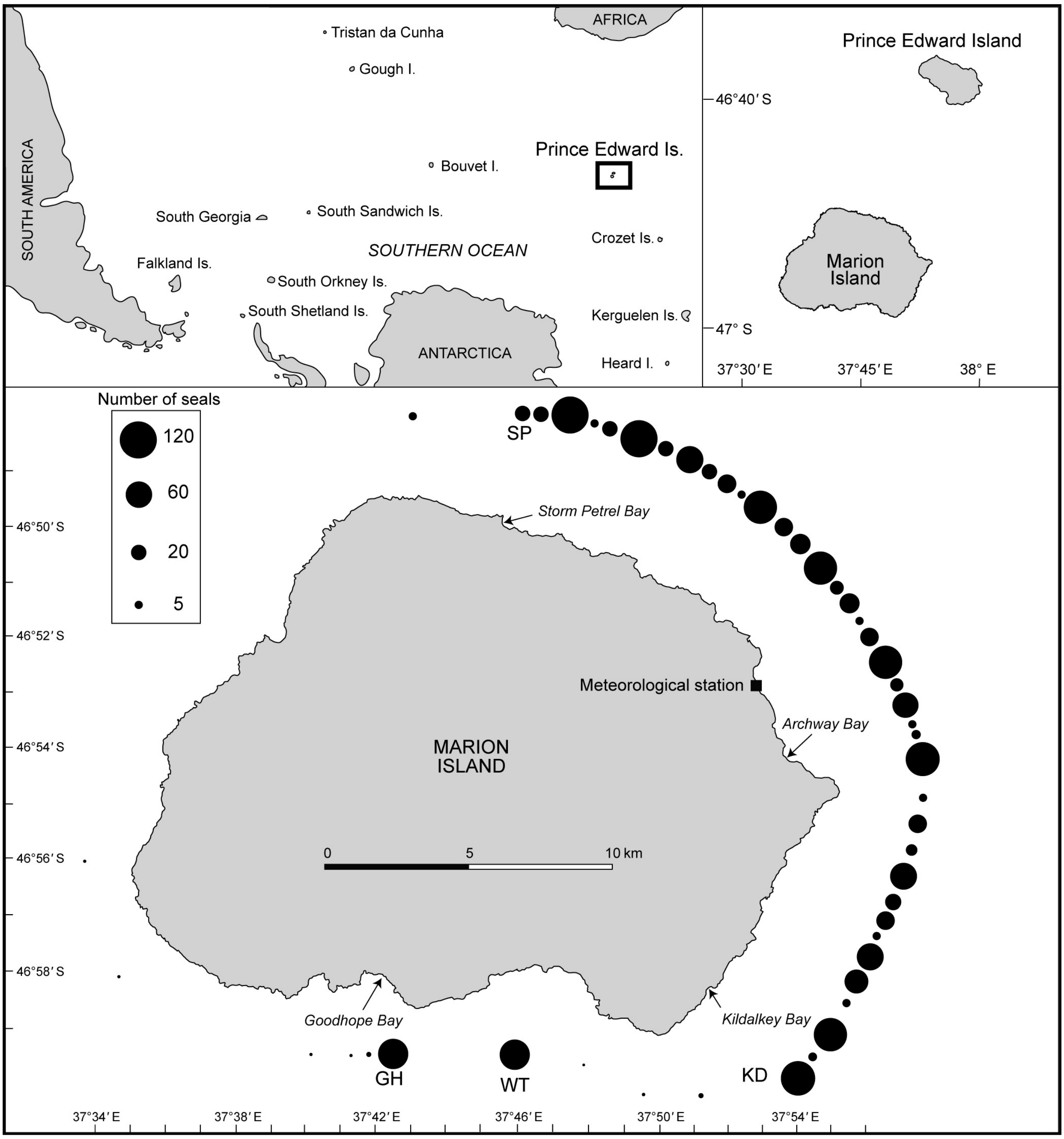

Figure 1.7 Map of Marion Island showing the distribution of southern elephant seals *Mirounga leonina*. The areas of the circles are directly proportional to the mean annual number of elephant seals hauling out at each site. The north and east sections of the coastline between locations marked SP and KD and at locations marked WT and GH form the study area. Reproduced from *African Journal of Marine Science* (2012) 34(3): 373-382 with permission © NISC (Pty) Ltd.

Most beaches are found on the leeward northern and eastern coasts. A number of beaches are also found on other coasts, those at Watertunnel and Goodhope Bay East being of greatest importance to elephant seals (Figure 1.7). Only one sandy and one shingle beach are found, the substrate of the other beaches being pebbles and boulders. These beaches vary in profile, some beaches, or parts of beaches, being far more level than others. Many of the beaches, especially those at which rivers flow out, are backed by vegetated areas of tussock grass and muddy pools and wallows. The beaches are relatively small (5 – 200 m sea front) and isolated from one another. Elephant seals must therefore enter the sea to move from one beach to another. On very rare occasions individuals have moved between adjacent beaches overland during the moult (pers. obs.). Elephant seals are most commonly found on the pebble, boulder, shingle or sand beaches during the breeding season and winter haulout, and in the vegetated areas during the moult (Condy 1979; Mulaudzi *et al.* 2008).

Climate

Latitude and isolation are the two most important factors determining the climate at the Prince Edward Islands. The archipelago lies some 230 kilometres north of the Antarctic Polar Front in the "Roaring Forties" of the Southern Ocean and is distant from the influence of continental landmasses. The climate is therefore subantarctic and oceanic. It varies little both seasonally and diurnally. The main features are (1) a low mean annual temperature (approximately 6°C), (2) little diurnal or seasonal variation in temperature, (3) high mean annual precipitation (approximately 2 000 millimetres) falling as either rain, sleet, snow or graupel depending on the season and altitude, (4) strong sustained westerly winds with regular gales, (5) high humidity, and (6) a high degree of cloud cover (annual sunshine being only 30 % of the maximum possible)

(Schulze 1971). The islands are subject to global climate change (Smith & Steenkamp 1990; Le Roux 2008) with the mean sea surface temperature increasing by 1.4°C over the last half century (Mélice *et al.* 2003) and total annual precipitation decreasing from approximately 3 000 millimetres to 2 000 millimetres between 1960 and 2000 (Le Roux & McGeoch 2008).

The study of movement in pinnipeds

Information on the patterns of movement shown by pinnipeds comes from a number of sources. These include records of vagrants, repeat observations of animals with naturally distinguishing marks and anthropogenically marked animals, movements of animals carrying VHF transmitters, movements of animals carrying Geolocation Time Depth Recorders (GLTDRs) or satellite linked Platform Transmitter Terminals (PTTs), and genetic studies. The type of information generated by these sources is generally very different but often complementary (Boyd 2002).

The dispersal of pinnipeds has been the subject of two reviews and one brief summary. Baker (1978) used early sources of information to compare the dispersal of 12 species of seals. For only three of these were data generated by individually marked individuals. Patterns of dispersal were inferred for the others from sightings of vagrants, seasonal movements and the appearance of incipient colonies. Reidman (1990) summarised data on the movement of pinnipeds in a table that dealt primarily with migration. She noted that five showed evidence of substantial philopatry and that another showed some degree of philopatry.

Boyd (2002), however, considered the dispersal of both pinnipeds and seabirds, but rather than examining the patterns of dispersal of individual species, he attempted to draw broad conclusions and relate these to characteristics of life history and habitat. He noted that many studies show that, while there is a high degree of philopatry among pinnipeds, considerable dispersal takes place. These studies also indicate the importance of dispersal in terms of population dynamics, potentially leading to the colonisation of new rookeries or the recolonisation of extinct rookeries. Boyd (2002) also noted that the degree of site fidelity and other characteristics of dispersal among pinnipeds varies from species to species, and with different conditions, such as disturbance, predation and the level of environmental stability. He further stated that there is evidence to suggest that seals and seabirds that travelled short distances in the pursuit of prey tended to disperse farther than long-distance migrants, possibly because dispersal by the latter was less likely to result in changes in access to prey. Finally, he noted the difficulties that the study of dispersal of pinnipeds presented and suggested that detailed patterns of dispersal were unlikely to be revealed.

A search of the literature indicates that, while data on dispersal have been generated for many species of pinnipeds, seven species have come to the fore in terms of the details of patterns of dispersal shown: Northern fur seals *Callorhinus ursinus*, Antarctic fur seals *Arctocephalus gazella*, grey seals *Halichoerus grypus*, Weddell seals *Leptonychotes weddellii*, harbour seals *Phoca vitulina* and northern and southern elephant seals. Since the patterns of dispersal vary widely among species and groups of species, I discuss the evidence for dispersal for each of these under separate headings. In addition, while information on fidelity to marine foraging grounds by some of these species has also recently become available (for example Bradshaw *et al.* 2004), this aspect of pinniped movement is outside of the ambit of this review, which concentrates on fidelity to, and dispersal between terrestrial haulout sites.

Northern fur seals and Antarctic fur seals

Early studies of dispersal in otariids have mostly concerned Northern fur seals and Antarctic fur seals. These two species of otariids have very similar life histories and show similar patterns of dispersal, characterised by accuracy of return to previous breeding sites (Lunn & Boyd 1991; Baker *et al.* 1995). Individual northern fur seals move among existing major breeding haulouts (Kenyon 1960; Peterson *et al.* 1968; Griben 1979; Aschepkov & Kuzin 1986, 1987). However, the majority of these animals do so only when immature (Baker *et al.* 1995) and the extent to which they do so is readily affected by prevailing weather conditions (Lea *et al.* 2009). It was initially assumed that the number of these animals that bred at the site to which they transferred was very limited (Peterson *et al.* 1968), but genetic evidence indicates that as many as 85 % of individuals at small rookeries are born elsewhere (Pinsky *et al.* 2010). This species therefore exists in a single panmictic population with high levels of genetic diversity and low population structuring (Pinsky *et al.* 2010), and has established new colonies during the last half-century (Peterson *et al.* 1968). Despite this, low levels of natal dispersal characterise the behaviour of females at large northern fur seal rookeries (Baker *et al.* 1995). Furthermore, adult females show very high levels of breeding site fidelity, frequently hauling out within metres of the sites at which they had pupped in previous years (Kenyon 1960; Baker *et al.* 1995). This species shows sex bias in site fidelity; while males also show both natal and breeding site fidelity (Gentry 1998; Kiyota 2005), they disperse farther than adult females (Baker *et al.* 1995). This may be, at least partially, due to the occupation of progressively higher quality territories with each successive breeding season (Kiyota 2005).

Antarctic fur seals also show remarkable feats of site fidelity, with females hauling out only metres from sites where they have pupped previously (Lunn & Boyd 1991). Antarctic fur seal males, however, also show high levels of site fidelity, higher levels, in fact, than those of adult females (Hoffman *et al.* 2006). Identification of individuals by genetic means has indicated that almost half of males occupy breeding territories within a body length, and some 80 % within six metres of the site held the previous year (Hoffman *et al.* 2006). These males also disperse little within a breeding season (Hoffman *et al.* 2006). Unfortunately this study could only examine breeding site fidelity and not natal site fidelity.

Other otariids

While early studies of dispersal in otariids mostly concerned Northern fur seals and Antarctic fur seals, some degree of site fidelity was recorded for other species, including Cape fur seals *A. pusillus* (Rand 1959; Oosthuizen 1991), New Zealand fur seals *A. forsteri* (Stirling 1971), South American fur seals *A. australis* (Harcourt 1992), Australian sea lions *Neophoca cinerea* (Higgins & Gass 1993), Hooker's sea lions *Phocarctos hookeri* (Beentjes 1989) and California sea lions *Zalophus californianus* (Ridgway & Robison 1985). Recent studies have revealed greater detail of the dispersal of some of these otariids. These indicate high levels of site fidelity for Hooker's sea lions, with male biased dispersal (Robertson *et al.* 2006; Chilvers & Wilkinson 2008). California sea lions also show male biased dispersal, with males dispersing 6.75 times more often than females (González –Suárez *et al.* 2009). Galapagos sea lions *Zalophus* *wollebaeki* also show high levels of site fidelity, but equal levels for both males and females (Wolf & Trillmich 2007). These animals frequently breed within metres of previously visited sites but show less site fidelity during non-breeding haulouts (Wolf & Trillmich 2007).

Grey seals

Among phocids, site fidelity has been examined most extensively in grey seals. The most important studies are those concerning both large and small scale movements, and site selection, at the island of North Rona and the Isle of May, Scotland. At these sites, adult females seldom change their pupping locations between years, although one individual was recorded to give birth 160 kilometres from her previous pupping site (Pomeroy *et al.* 1994). The majority of adult female grey seals that pupped at their prior haulout beach did so within 50 metres of their prior pupping site (Pomeroy *et al.* 1994). A number of females moved several times before settling at a specific pupping site (Anderson *et al.* 1975; Pomeroy *et al.* 1994). Adult females also showed substantial, but lower levels of natal site fidelity (Pomeroy *et al.* 2000b). Analysis of genetic evidence supports these conclusions, indicating higher levels of relatedness within rookeries than among rookeries (Poland *et al.* 2008).

Male seals also showed high site fidelity, breeding half the randomly generated expected distance from their previous breeding site. The levels of site fidelity for males were not related to social and life history factors, such as dominance level, reproductive success, or timing of the breeding haulout (Twiss *et al.* 1994). Site fidelity is greater at North Rona than at the Isle of May, possibly because topography constrains seals to a limited number of locations at North Rona but not at the latter island (Pomeroy *et al.*

2000a; Pomeroy *et al.* 2000b). Other topographical features are also important, with adult females choosing to breed near pools, most likely for thermoregulatory purposes (Redman *et al.* 2001; Twiss *et al.* 2002). In addition to site fidelity, genetic work has also indicated that adult female grey seals choose both to associate with other known adult females (Pomeroy *et al.* 2005) and show fidelity to mates (Amos *et al.* 1995; Twiss *et al.* 2006).

Studies of grey seals at other sites have shown that while most young seals haul out within 100 kilometres of their natal site, many dispersed farther, some as far as 1000 kilometres (Bjørge & McConnell 1986; Wiig & Øien 1987; Björge *et al.* 2002). Baker (1978) assumed that the majority of these animals returned to their natal population, although the establishment of new rookeries indicates that some animals must breed away from their natal rookery (T'Hart *et al.* 1988). Considering the movement of older animals, Boness & James (1979) noted an average dispersal distance of 18 m between successive breeding seasons for adult females at Sable Island, Canada. Vincent *et al.* (2005) also examined breeding site fidelity of grey seals, and showed an inter-annual fidelity of between 70 and 95 % at the Molène Archipelago, France.

Weddell seals

Large numbers of Weddell seals have been tagged in the Ross Sea and at Signy Island, Antarctica (Stirling 1969; Croxall & Hiby 1983; Testa 1987a). Females of both of these populations show relatively low natal site fidelity (Croxall & Hiby 1983; Testa 1987b, a; Cameron *et al.* 2007) but much higher breeding site fidelity (Stirling 1969, 1974; Croxall & Hiby 1983; Testa 1987a; Cameron *et al.* 2007). The majority of dispersing individuals were immature animals and young adult females (Stirling 1974; Croxall &

Hiby 1983; Testa 1987b) and site fidelity increased with age (Cameron *et al.* 2007). While dispersal among rookeries takes place (Stirling 1969; Croxall & Hiby 1983; Testa 1987a), a considerable portion is temporary (Cameron & Siniff 2004). Evidence indicates that emigration is linked to prevailing sea-ice conditions with greater levels in years when the extent of sea-ice is less and therefore putative preferred haulout areas not available (Cameron & Siniff 2004). Most adult females returned to breed in the area in which they had pupped in the previous year, or the neighbouring site (Stirling 1974; Croxall & Hiby 1983; Testa 1987b). The degree of site fidelity by females, however, was linked to reproductive success (Cameron *et al.* 2007). Although the dispersal of male Weddell seals has been examined less often than that of females, that which has been done indicates no difference in breeding site fidelity between the sexes (Cameron *et al.* 2007). High site fidelity of males is also likely at other sites around Antarctica (Terhune *et al.* 2008). Low breeding dispersal of this sex is postulated to confer advantages in terms of reproductive success due to greater familiarity with a particular site (Harcourt *et al.* 2007). Familiarity will allows males to defend tidal cracks in fast ice, which provide access to breeding areas and the location of which remains relatively consistent between years (Harcourt *et al.* 2007). In addition, familiarity with predictable foraging hotspots (Hindell *et al.* 2002) may increase the reproductive success of this species since mating is aquatic (Harcourt *et al.* 2007).

Harbour seals

Foraging harbour seals *Phoca vitulina* seldom move farther than 100 kilometres from their tagging site (Bonner & Witthames 1974; Thompson & Miller 1990; Thompson *et al.* 1994a; Thompson *et al.* 1994b; Lesage *et al.* 2004; Cunningham *et al.* 2009) and dispersal distances are also generally shorter than for other species of seals (Bonner &

Witthames 1974; Thompson *et al.* 1994a). Those few animals that do move substantial distances are primarily immature animals (Thompson 1989). There is, however, little evidence of permanent emigration (Bonner & Witthames 1974). On a finer scale, fidelity is to specific rookeries, but not to locations within a rookery (Schaeff *et al.* 1999). Evidence indicates that haulout site selection is influenced by various aspects of habitat quality including anthropogenic disturbance (Cunningham *et al.* 2009; Becker *et al.* 2011; Blundell *et al.* 2011).

Other phocids

Interannual breeding site fidelity has been recorded for ringed seals *Phoca hispida* (Kelly *et al.* 2010), and bearded seals *Erignathus barbatus* (Van Parijs & Clark 2006). Many studies have indicated that the predominant dispersers are immature animals in hooded seals *Cystophora cristata* (Hammill 1993) and leopard seals *Hydrurga leptonyx* (Jessopp *et al.* 2004; Forcada & Robinson 2006). For hooded seals there is little evidence of permanent emigration (Hammill 1993). Among ringed seals, dispersal is linked to sea-ice conditions (Kelly *et al.* 2010).

Elephant seals

The dispersal capabilities and patterns of dispersal of elephant seals have been both noted frequently and anecdotally and have been the subject of several studies. Vagrant elephant seals are frequently recorded (Kettlewell & Rand 1955; Ingham 1957; Ross 1969; Best 1971; Mills *et al.* 1977; Murray 1981; Heimark & Heimark 1986; Oosthuizen *et al.* 1988; Taylor & Taylor 1989; Alava & Carvajal 2005; De Moura *et al.* 2010). The maximum distances that vagrants have travelled from the closest possible sites of origin are 11 000 kilometres for the northern species (Kiyota *et al.* 1992), and

9 000 kilometres for the southern species (Johnson 1990). The majority of vagrants are, however, not tagged and their locations of origin are therefore not known. While these animals indicate that elephant seals are capable of moving vast distances, only tagged individuals, or genetic analysis, are able to indicate potential movement among different populations and metapopulations. The movement of marked vagrants, and the movement of marked animals among populations, are therefore more interesting and a number of such movements have been recorded (Vaughan 1967; Burton 1985; Bester 1988, 1989; Guinet *et al.* 1992; Hindell & McMahon 2000; Van den Hoff 2001; Reisinger & Bester 2010; Oosthuizen *et al.* 2011). The furthest recorded distance moved by a marked animal is 5 200 kilometres, for a seal that moved between its natal site on Macquarie Island and Peter I Øy (Hindell & McMahon 2000). Further important records are those where females have given birth outside of their normal range on the coast of South Africa (Vaughan 1967; Oosthuizen *et al.* 1988), Amsterdam Island (Carrick & Ingham 1962a), Australia and New Zealand (Taylor & Taylor 1989), and Antarctica (McMahon & Campbell 2000). These records are significant, not only because they indicate the potential for the movement of genetic material among populations and metapopulations, but also because they indicate the potential for changes in geographical distribution. That such changes are possible can be seen from the re-establishment of historical breeding sites by the congeneric northern elephant seals following the cessation of intensive exploitation (Le Boeuf & Laws 1994). The range of the southern elephant seal has also changed, both in historical and prehistoric times. Palaeontological evidence indicates that breeding haulouts were found on the Antarctic continent between 7 500 and 1 000 years ago (Hall *et al.* 2006; de Bruyn *et al.* 2009). It is possible that current anthropogenic climate change may cause future expansion or contraction of the range of this species.

Characteristics of dispersal for northern elephant seals have been noted by a number of authors. Huber *et al*. (1991) indicated that 15 % of female seals at the South Farallon Islands, California, moved to a different location to pup for the first time but that no females pupped at a different site subsequently. Further support for dispersal being primarily by primiparous females is indicated by the immigration to the South Farallon Islands and Isla Año Nuevo from adjacent island groups by young females (Reiter *et al.* 1981; Huber *et al.* 1991). Le Boeuf *et al*. (1974) and Huber *et al*. (1991) also noted that the numbers of immigrants to the South Farallon Islands from other islands was inversely proportional to the distances to those islands. Stewart (1989) also indicated that it was the younger females that tended to move away from large harems.

Conducting the first in-depth study of southern elephant seal behaviour, Laws (1956) noted that adult male elephant seals hauled out at the same site during successive breeding seasons at the island of South Georgia. He identified these animals based on natural markings. Apart from this observation he did not follow these animals any further. Dispersal of this species has been examined in greater detail at a number of sites. At Macquarie Island, the resighting of branded seals over a number of years has yielded considerable data. This indicates that adult females show limited natal dispersal, frequently breeding close to or at their natal site (Carrick & Ingham 1962b). Comparing the sexes, males show less site fidelity than females, but this concerns breeding dispersal alone (Carrick & Ingham 1962a; Nichols 1970). Natal site fidelity was not evident during moult and winter haulouts, except in young adult females (Nichols 1970). Elephant seals at Macquarie Island also showed long-term site fidelity, with females of over 20 years of age hauling out close to the natal sites (Hindell & Little 1988).

The movements of under-yearlings has been examined at the Îles Kerguelen where Lenglart & Bester (1982) found no significant differences between males and females of this age class. They noted, furthermore, that movements were largely dependent on prevailing inshore wave and wind direction. Among adults, females showed significant natal site fidelity during the breeding season (Bester & van Niekerk 1984). The location of moult haulouts, however, was influenced by the location of habitat type (Setsaas *et al.* 2008). Many animals moved among sites during a single moult haulout, primarily to sites farther from their natal site (Setsaas *et al.* 2008). During this season immature animals dispersed farther than adults. Although no difference in site fidelity during the moult was found between the sexes, males moved farther than females during the breeding season (Bester & van Niekerk 1984).

The elephant seal population at Peninsula Valdés is more spread out than other populations, which has some influence on the patterns of dispersal. Although some individuals breed or moult farther than 100 kilometres from their natal site, or the site at which they were marked as an adult (Campagna & Lewis 1992), most do so far closer (Lewis *et al.* 1996). Although animals from this population have been recorded moulting among the elephant seal population at the Falkland Islands, none have been recorded breeding there (Lewis *et al.* 1996; Galimberti & Sanvito 1999). Fabiani *et al.* (2006) examined site fidelity at the Falklands Island population itself and noted high levels of site fidelity, but significantly male biased dispersal. They also noted that dispersal by females was not related to the size of breeding aggregations.

Southern elephant seals haul out to moult on the coast of Antarctica at the Vestfold Hills (Tierney 1977; Burton 1985; Bester 1988) and Windmill Islands (Van den Hoff *et al.* 2003) despite being born over 2500 kilometres distant on Îles Kerguelen, Heard Island

and Macquarie Island. Some 40 % of tagged seals moulting at the Vestfold Hills return in subsequent seasons, thus showing fidelity to a moult site distant from their natal site (Gales & Burton 1989). While these animals are primarily subadult and adult males, adult females have been seen and occasional pupping has been recorded (McMahon & Campbell 2000).

Various aspects of site fidelity have been examined at Marion Island. Mulaudzi *et al.* (2008) noted that elephant seals prefer certain locations as haulout sites, while avoiding others. Sites selected depended on age and sex class, and type of haulout. Post weaning movements of pups were examined by Panagis (1981) and Wilkinson & Bester (1990). They found that few pups moved away from their natal site between weaning and their first extended marine period. For those that did move away, the distance displaced increased with time after weaning. Wilkinson & Bester (1990) noted that males were the predominant and furthest dispersers.

Examination of site fidelity of older animals was made possible by a long-term mark-recapture programme for the population on Marion Island itself. Movements to neighbouring Prince Edward Island (Oosthuizen *et al.* 2009) and other archipelagos (Oosthuizen *et al.* 2011) were necessarily ignored in this analysis because of the low levels of resolution provided by the relatively few data collected at these sites. All interpretations must bear this in mind (Hofmeyr 2000). Hofmeyr (2000) assessed the movements of 12 cohorts of animals using these data and found that all age and sex classes showed greater fidelity than expected to their natal site during winter, moult and breeding haulouts. Adult animals, however, showed greater fidelity to their first breeding haulout site than to their natal site, when they returned to breed or to moult. A sex bias in dispersal was further evident for breeding haulouts, with males showing greater philopatry than females. This is unusual for mate defence polygynous mammals. While genetic evidence indicates male biased dispersal (Fabiani *et al.* 2003; Chauke 2009), this is for movements among island groups rather than at a single island. While the sex bias in dispersal at Marion Island itself may be related to the nature of the relatively even distribution of resources during the breeding season, and therefore the lack of advantage gained by females from philopatry, Hofmeyr (2000) ascribed it to the greater mobility of males during this season. They are not limited to the first or second site that they visit after a winter at sea, whereas females are, since they give birth to a relatively immobile pup within days of arrival. Males are therefore able to move among sites during the breeding season, and they frequently do so (Munyai 2006) which allows them to be more site selective. Sex bias in site fidelity was not evident during winter and moult haulouts, however (Hofmeyr 2000). Natal site fidelity was also significantly greater during the breeding haulout than either the winter or moult haulout, but no difference in natal site fidelity was apparent between the latter two seasons, despite a difference in habitat used (Hofmeyr 2000).

Hofmeyr (2000) showed that a number of other factors influence site fidelity at Marion Island. Age was one of these. Amongst first-time breeding females, older animals hauled out farther from their natal site than younger animals. When hauling out for the winter or moult, however, older animals showed greater natal site fidelity. Site isolation also affected site fidelity with animals from the more isolated beaches dispersing farther. Anthropogenic disturbance was a further significant influence. While breeding animals from more disturbed sites hauled out farther from their natal site than those from less disturbed sites, as expected, animals hauling out during the winter or to moult actually hauled out closer to the more anthropogenically disturbed sites. It is possible that immature seals engaged in these haulouts do so, so as to avoid sites that are more disturbed by breeding elephant seals. Finally, dispersal is also influenced by natal harem size, with animals born in smaller harems dispersing farther. This is possibly because site popularity is an indication of site quality, or simply because large groups are more attractive. Seals may therefore tend to select larger harems.

Aims of the study

Overview

While the studies noted above consider various aspects of dispersal, site fidelity and site selection by southern elephant seals, they do so only in relation to the animal's natal or first reproductive haulout site. These studies therefore ignore the influence of the many other sites that seals may have visited over the course of their lives. In this study I aim to provide a more complete picture by attempting to identify patterns of dispersal by individual southern elephant seals at Marion Island in relation to all past haulout sites used by those individuals. I attempt to answer a number of questions related to the selection of a terrestrial site. Firstly, what aspect, if any, of a southern elephant seal's history of haulouts at Marion Island determine the sites that they choose as their next haulout? Are they merely hauling out at random at any site on Marion Island, or are the sites that they choose related to any previous sites? Are they attempting to return to any particular site? If so, which previous site? Previously, I indicated that natal sites are important, that is, that they are returning closer to their natal site than could be expected by chance alone (Hofmeyr 2000). It seems that they are making an effort to return to their natal site. However, are any other sites that they have visited of equal or greater importance?

Secondly, I ask what makes a site important. What characteristics of a haulout event does a seal remember when it subsequently returns to Marion Island and chooses to haul out at, or close to that site? The characteristics referred to here are those related to the age of the animal and the haulout type, and not to the topographic characteristics and popularity of the sites themselves (as examined by Mulaudzi 2005; Mulaudzi *et al.* 2008). Therefore I ask if the fact that a seal visited a site at a particular age, or for a particular type of haulout, or a particular type of haulout at a particular age, is important in its return to, or to the vicinity of that site. For example, is the site that it visited as a yearling important in determining where it subsequently hauls out, or is the site that it moulted at important, or is the site that it moulted at as a yearling important?

This leads to a third question: are the present age and sex of the seal, and the present type of haulout important in determining which of its past experiences are relevant? Do past haulouts of a particular type at a particular age only influence present haulouts of a particular age and type for animals of a particular sex? For example, for a hypothetical female elephant seal, was the site which it visited to moult at as a yearling important in determining where it hauled out as an immature animal, but was its natal site important in determining where it hauled out to breed for the first time as a four-year-old? Furthermore, was the first site at which it hauled out to breed important in determining where it hauled out to breed subsequently, but its previous moult site important in determining where it hauled out to moult subsequently?

A fourth question concerns the purpose of the winter haulout. While it is obvious why elephant seals haul out during the breeding season and the moult, the reasons for winter haulouts undertaken by immature individuals are unknown. Various explanations have been advanced (reviewed in Burton 1985; Pistorius *et al.* 2002). Here I test one of these; that these haulouts assist elephant seals in maintaining familiarity with their natal site. I also test whether other haulouts undertaken as an immature assist in maintaining site familiarity.

Finally, I further question site familiarity and site fidelity. I examine deterioration in spatial memory over time by examining the effects of duration between visits to a site, and the number of visits to that site.

Further fascinating questions which are beyond the scope of this study, and therefore which are not addressed here, include the effect on site fidelity of characteristics of a haulout event or haulout site. Among these are the following questions. 1. Are pup mortality, site popularity, site isolation, anthropogenic disturbance and section of the coastline important in determining whether a seal will subsequently attempt to return to a particular site? For example, will the behaviour of a female elephant seal from Marion Island follow the pattern described above unless she hauls out to breed at a site that is subject to high pup mortality, or at a site which is not popular, or at a site which experiences high anthropogenic disturbance? 2. Is any site good enough as a haulout site? Or is any site good enough as a moult or winter haulout site, but not as a breeding haulout site? Or is any site that meets a number of basic requirements good enough to be a haulout site? For example, one that is flat, popular and not exposed to high seas.

Therefore, should a seal haul out at such a site, it will remain at that site irrespective of where it has hauled out before, or where it has been born.

Key questions

I attempt to answer the broad questions noted above by asking the following key questions, each of which is addressed in a separate chapter:

1. Does the history of terrestrial site use by female southern elephant seals from Marion Island influence their choice of haulout sites? That is, do they show fidelity to any previous haulout sites other than their natal site and site of first reproductive haulout? (Chapter 2)
2. Does the history of terrestrial site use by male southern elephant seals from Marion Island influence their choice of haulout sites? That is, do they show fidelity to any previous haulout sites other than their natal site and site of first reproductive haulout? Does the pattern of fidelity shown differ from that of females? (Chapter 3)
3. Does participation in a winter haulout by female southern elephant seals serve to maintain fidelity to their natal site? (Chapter 4)
4. Does the duration of the period between visits to a site and the number of visits to a site affect fidelity to that site? (Chapter 5)

Null hypotheses

To answer the key questions the hypotheses below are tested:

1. Female southern elephant seals of the Marion Island population do not show significant fidelity to any previous haulout site other than their natal site and first

reproductive haulout site. The various previous haulout sites relevant to each current haulout site are listed in Table 1.3.

2. Male southern elephant seals of the Marion Island population do not show significant fidelity to any previous haulout site other than their natal site and first reproductive haulout site. The various previous haulout sites relevant to each current haulout site are listed in Table 1.4.
3. Participation in the winter haulout as an immature animal does not serve to maintain fidelity to the natal site.
4. The length of the duration between visits to a particular site and the number of visits to that site do not affect fidelity to that site.

Assumptions associated with this study

This study is subject to a number of assumptions.

1. These analyses only describe the site fidelity of elephant seals in the study area and do not take into account movement to neighbouring Prince Edward Island, which is also a haulout site for southern elephant seals, including those tagged at the study site (Bester 1989; Bester & Hofmeyr 2005; Oosthuizen *et al.* 2009) or to other locations farther a field. This assumption was specifically noted by Hofmeyr (2000) who stated “missing haulout events indicate that animals must use other sites, especially for the moult, which is an annual necessity”, the term “sites” being used in this quote to refer to other islands. Furthermore, the presence of tagged seals from the Îles Crozet on Marion Island (Bester 1989; Oosthuizen *et al.* 2011), and genetic evidence (Chauke 2009) indicates that movement to and from locations outside of the archipelago takes place. It is possible that the patterns of dispersal of animals

Table 1.3 Prior haulout sites against which assessment of current haulout site is tested for fidelity by female southern elephant seals *Mirounga leonina* at Marion Island. Abbreviations of types of terrestrial periods are as follows: N – natal period, W – winter haulout, M – moult haulout, B – breeding haulout, RHN1 – first reproductive haulout. These abbreviations are modified as follows to represent different haulout events: Pr – previous year's haulout, 0, 1, etc. – haulout events as underyearlings, yearlings, etc.

Current haulout site	Previous haulout sites													
RHN1	N	W0	M1	W1	M2	W2								PrM
RHN2	N	W0	M1	W1	M2	W2	M3					RHN1		PrM
RHN>2	N	W0	M1	W1	M2	W2	M3	M4				RHN1	PrB	PrM
B3 & B4 primiparous	N	W0	M1	W1	M2	W2								PrM
B5 & B6 primiparous	N	W0	M1	W1	M2	W2	M3	M4						PrM
B4 & B5 diparous	N	W0	M1	W1	M2	W2	M3					RHN1		PrM
B6 & B7 diparous	N	W0	M1	W1	M2	W2	M3	M4	M5			RHN1		PrM
B5 & B6 multiparous	N	W0	M1	W1	M2	W2	M3	M4				RHN1	PrB	PrM
B7 & B8 multiparous	N	W0	M1	W1	M2	W2	M3	M4	M5	M6		RHN1	PrB	PrM
M1	N	W0												
M2	N	W0	M1	W1										
M3 have not bred	N	W0	M1	W1	M2	W2								
M4 have bred	N	W0	M1	W1	M2	W2	M3					RHN1		
M5 have bred	N	W0	M1	W1	M2	W2	M3	M4				RHN1	PrB	
M6 have bred	N	W0	M1	W1	M2	W2	M3	M4	M5			RHN1	PrB	
M7 have bred	N	W0	M1	W1	M2	W2	M3	M4	M5	M6		RHN1	PrB	
M8 have bred	N	W0	M1	W1	M2	W2	M3	M4	M5	M6	M7	RHN1	PrB	
W1	N	W0	M1											
W2	N	W0	M1	W1	M2									

Table 1.4 Prior haulout sites against which assessment of current haulout site is tested for fidelity by male southern elephant seals *Mirounga leonina* at Marion Island. Abbreviations of types of terrestrial periods are as follows: N – natal period, W – winter haulout, M – moult haulout, B – breeding haulout, RHN1 – first reproductive haulout. These abbreviations are modified as follows to represent different haulout events: Pr – previous year's haulout, 0, 1, etc. – haulout events as underyearlings, yearlings, etc.

Current haulout site	Previous haulout sites																	
Male RHN1	N	W0	M1	W1	M2	W2	M3	W3	M4	W4	M5	W5						PrM
Male RHN2	N	W0	M1	W1	M2	W2	M3	W3	M4	W4	M5	W5	M6			RHN1		PrM
Male RHN>2	N	W0	M1	W1	M2	W2	M3	W3	M4	W4	M5	W5	M6	M7		RHN1	PrB	PrM
Male B6 1st time breeders	N	W0	M1	W1	M2	W2	M3	W3	M4	W4	M5	W5						PrM
Male B7 1st time breeders	N	W0	M1	W1	M2	W2	M3	W3	M4	W4	M5	W5	M6					PrM
Male B7 2nd time breeders	N	W0	M1	W1	M2	W2	M3	W3	M4	W4	M5	W5	M6			RHN1		PrM
Male B>7 2nd time breeders	N	W0	M1	W1	M2	W2	M3	W3	M4	W4	M5	W5	M6	M7		RHN1		PrM
Male B8 & B9 - bred > twice	N	W0	M1	W1	M2	W2	M3	W3	M4	W4	M5	W5	M6	M7		RHN1	PrB	PrM
Male B>9 - bred > twice	N	W0	M1	W1	M2	W2	M3	W3	M4	W4	M5	W5	M6	M7	M8	RHN1	PrB	PrM
Male M1	N	W0																
Male M2	N	W0	M1	W1														
Male M3	N	W0	M1	W1	M2	W2												
Male M4	N	W0	M1	W1	M2	W2	M3	W3										
Male M5	N	W0	M1	W1	M2	W2	M3	W3	M4	W4								
Male M6 have not bred	N	W0	M1	W1	M2	W2	M3	W3	M4	W4	M5	W5						
Male M7 have bred	N	W0	M1	W1	M2	W2	M3	W3	M4	W4	M5	W5	M6			RHN1	PrB	
Male M8	N	W0	M1	W1	M2	W2	M3	W3	M4	W4	M5	W5	M6	M7		RHN1	PrB	
Male W1	N	W0	M1															
Male W2	N	W0	M1	W1	M2													
Male W3	N	W0	M1	W1	M2	W2	M3											
Male W4	N	W0	M1	W1	M2	W2	M3	W3	M4									
Male W5	N	W0	M1	W1	M2	W2	M3	W3	M4	W4	M5							

born on Marion Island, but that haul out on Prince Edward Island and elsewhere, are different to those of animals that are philopatric, but assessing this is beyond the scope of this study. Ultimately, the proportion of seals that transfer from the study site is unknown (Oosthuizen *et al.* 2011) since resight programmes exist at those sites. Since Prince Edward Island is managed as a Protected Zone with limited entry (PEIMPWG 1996), it is not possible to assess movement among the islands with a suitable degree of resolution to adequately examine patterns of intra-archipelago dispersal (Oosthuizen *et al.* 2009).

2. The number of seals hauling out on Marion Island outside of the 40 beaches of the study area is assumed to be negligible and to have no impact on the study. This is a reasonable assumption since these sites are unsuited to elephant seals due to their rough topography and windward aspect. Although these sites are generally not visited regularly (less than once per month) very few seals are noted on them. Over the 21 years of the study (1983 – 2004) only 267 haulouts have been recorded at these sites. This is 0.34 % of all records collected. Most on these (103) are from the main beach at Cape Davis which is the only one relatively suited to elephant seals and the only one visited regularly (monthly).
3. Missing seals due to their movement between sites during the course of a census, which takes place over 2 – 5 days, is assumed to be negligible. Munyai (2006) indicated that movements between sites during a haulout is negligible. For most haulout types, and age and sex classes, the number of moves between sites was less than 0.4. The exception was adult males ashore for the breeding season, which nevertheless only moved an average of 1.01 during a haulout.
4. Tag loss was assumed to be minimal and removed relatively few animals from the population. Oosthuizen *et al.* (2010) noted that the loss of both tags during the first

five years of age was less than 1 % for the majority of animals (see comment on differences between cohorts below). They also estimated that 98 % of female seals and 96 % of male seals would retain at least one tag up to age eight.

5. Cohort is assumed to have no effect on the results and data for separate cohorts were pooled. This is a reasonable assumption since Hofmeyr (2000) found little evidence for differences in natal or first breeding site fidelity among cohorts of elephant seals at the study site. Furthermore, de Bruyn (2009) stated that "We found no significant differences in resight probability among cohorts of adult female southern elephant seals at Marion Island and hence conclude that all seals had the same chance of being resighted during the study". While Oosthuizen *et al*. (2010) described increased cohort dependent tag-loss rates for the Marion Island elephant seal population in the last four cohorts used in this study, these are only responsible for 11 % of all data analysed and 0.02 % of the data analysed for adults.
6. Resight effort is assumed to remain constant for the duration of the study and unaffected by changes in observers among years or by changes in observer experience and motivation within years. Some differences are possible, however, since prior to 1989 tag resights were limited to the period August to May. However, relatively few seals haul out at the study site during the excluded months. Possible factors affecting resight effort and sightability are discussed in detail in de Bruyn (2009).
7. It is assumed that age and sex class did not influence resight probability. This is unlikely. Oosthuizen *et al*. (2010) showed sex dependent differences in tag loss probability with adult males being more likely to have lost tags than adult females. In addition, the tags of males and adult animals are frequently more difficult to read because of the larger size of their hind flippers and differences in behaviour (pers. obs.). It is possible, however, that this did not significantly impact on the data since the

frequency of resight sessions allowed for animals to be resighted several times during a haulout event.

8. The resight probability of animals during the different haulouts is assumed to be identical. This is unlikely since the behaviour of animals during the breeding season makes reading tags at this time more difficult than during the winter and the moult haulouts. However, resight frequency was increased by a third during the breeding season, and considerably longer periods were spent trying to read tags, all of which would mitigate against a seasonal bias. It is also possible that some seals were missed during the moult due to their propensity to move inland at this time of the year. This was also mitigated against by searches of likely inland moult areas.
9. The observers are assumed to have read tags numbers and identified tag colours correctly. The database does contain obviously incorrect records, for example, a single record of an individual as a female with pup amongst the lifetime of records of a seal that was otherwise consistently recorded as a male, but these are few. Where possible, erroneous records were identified and excluded. The opportunity to check records by comparing the size of animals bearing tags of a particular colour to others of that cohort, and to identify sex, acted as mechanisms for maintaining the quality of tag resights.
10. The topography of sites is assumed not to have biased resight probability. Although it is possible that some seals escaped observation at sites with more complex topography (especially at sites that extend inland), a thorough knowledge of all sites learnt by observers prior to the onset of the breeding season and the use of standard search patterns should have prevented seals from escaping observation.
11. Each haulout is assumed to be independent of all others and therefore haulouts by the same individual were treated as unrelated and were grouped in a sample.
12. Since animals were frequently recorded more than once during a haulout event (an average of 2.00 times), and sometimes at different sites, a representative record had to

be selected. It is assumed that the criteria used to select representative records was able to identify the most important site.

References

ALAVA, J.J. & CARVAJAL, R. 2005. First records of elephant seals on the Guayaquil Gulf, Ecuador: on the occurrenc of either a *Mirounga leonina* or *M. angustirostris*. *Latin American Journal of Aquatic Mammals* **4:** 195-198.

AMOS, B., TWISS, S., POMEROY, P. & ANDERSON, S. 1995. Evidence for mate fidelity in the gray seal. *Science* **268:** 1897-1899.

ANDERSON, S.S., BURTON, R.W. & SUMMERS, C.F. 1975. Behaviour of grey seals (*Halichoerus grypus*) during a breeding season at North Rona. *Journal of Zoology, London* **177:** 179-195.

ASCHEPKOV, A.T. & KUZIN, A.E. 1986. Mixing, routes and time of migration of fur seals of different stocks in the Pacific waters of Japan. *Biologiya Morya (Vladivistok)* **0 (6):** 26-32.

ASCHEPKOV, A.T. & KUZIN, A.E. 1987. Age and sex structure of fur seal stocks migrating to the Pacific waters of Japan. *Biologiya Morya (Vladivistok)* **0 (2):** 29-38.

AUTHIER, M., DELORD, K. & GUINET, C. 2011. Population trends of female elephant seals breeding on the Courbet Peninsula, Îles Kerguelen. *Polar Biology* **34:** 319-328.

BAKER, J.D., ANTONELIS, G.A., FOWLER, C.W. & YORK, A.E. 1995. Natal site fidelity in northern fur seals, *Callorhinus ursinus*. *Animal Behaviour* **50:** 237-247.

BAKER, R.B. 1978. *The ecology of animal migration.* Hodder and Stoughten, London. 967 pp.

BARTHOLOMEW, G.A. & HUBBS, C.L. 1960. Population growth and seasonal movements of the northern elephant seal, *Mirounga angustirostris*. *Mammalia* **24:** 313-324.

BECKER, B.H., PRESS, D.T. & ALLEN, S.G. 2011. Evidence for long-term spatial displacement of breeding and pupping harbour seals by shellfish aquaculture over three decades. *Aquatic Conservation: Marine and Freshwater Ecosystems* **21:** 247-260.

BEENTJES, M.P. 1989. Haul-out patterns, site fidelity and activity budgets of male Hooker's sea lions (*Phocarctos hookeri*) on the New Zealand mainland. *Marine Mammal Science* **5:** 281-297.

BELETSKY, L.D. & ORIANS, G.H. 1991. Effects of breeding experience and familiarity on site fidelity in female red-winged blackbirds. *Ecology* **72:** 787-796.

BEST, P.B. 1971. Stalked barnacles *Conchoderma auritum* on an elephant seal: occurrence of elephant seals on the South African coast. *Zoologica Africana* **6:** 181-185.

BESTER, M.N. 1980. The southern elephant seal *Mirounga leonina* at Gough Island. *South African Journal of Zoology* **15:** 235-239.

BESTER, M.N. 1988. Marking and monitoring studies of the Kerguelen stock of southern elephant seals *Mirounga leonina* and their bearing on biological research in the Vestfold Hills. *Hydrobiologia* **165:** 269-277.

BESTER, M.N. 1989. Movements of southern elephant seals and Subantarctic fur seals in relation to Marion Island. *Marine Mammal Science* **5:** 257-265.

BESTER, M.N. & HOFMEYR, G.J.G. 2005. Numbers of elephant seals at Prince Edward Island, Southern Ocean. *South African Journal of Wildlife Research* **35:** 85-88.

BESTER, M.N., MÖLLER, H., WIUM, J. & ENSLIN, B. 2001. An update on the status of southern elephant seals at Gough Island. *South African Journal of Wildlife Research* **31:** 68-71.

BESTER, M.N. & PANSEGROUW, H.M. 1992. Ranging behaviour of southern elephant seal cows from Marion Island. *South African Journal of Science* **88:** 574-577.

BESTER, M.N. & VAN NIEKERK, J.L. 1984. *Dispersie van suidelike olifantrobbe Mirounga leonina te die Courbet Skiereiland, Iles Kerguelen*. Internal report, Mammal Research Institute, University of Pretoria, Pretoria. 41 pp.

BESTER, M.N. & WILKINSON, I.S. 1994. Population ecology of southern elephant seals at Marion Island. In: *Elephant seals: population ecology, behavior and physiology*, (ed) B.J. Le Boeuf & R.M. Laws, pp. 85-97. University of California Press, Berkeley.

BJØRGE, A., BEKKBY, T., BAKKESTUEN, V. & FRAMSTAD, E. 2002. Interactions between harbour seals, *Phoca vitulina*, and fisheries in complex coastal waters explored by combined Geographic Information System (GIS) and energetics modelling. *ICES Journal of Marine Science* **59:** 29-42.

BJØRGE, A. & MCCONNELL, B. 1986. Gjenfangster i Norge av havert merket i Storbritannia. *Fisken og Havet* **2:** 1-8.

BLUNDELL, G.M., WOMBLE, J.N., PENDLETON, G.W., KARPOVICH, S.A., GENDE, S.M. & HERREMAN, J.K. 2011. Use of glacial and terrestrial habitats by harbor seals in Glacier Bay, Alaska: costs and benefits. *Marine Ecology Progress Series* **429:** 277-290.

BONESS, D.J. & JAMES, H. 1979. Reproductive behaviour of the grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. *Journal of Zoology, London* **188:** 477-500.

BONNER, W.N. 1989. *The biology of seals.* Christopher Helm, Bromley, United Kingdom. pp.

BONNER, W.N. & WITTHAMES, S.R. 1974. Dispersal of common seals (*Phoca vitulina*), tagged in the Wash, East Anglia. *Journal of Zoology, London* **174:** 528-531.

BOYD, I.L. 2002. The measurement of dispersal by seabirds and seals: implications for understanding their ecology. In: *Dispersal Ecology*, (ed) J.M. Bullock, R.E. Kenward & R.S. Hails, pp. 480. Cambridge University Press, Cambridge.

BOYD, I.L., WALKER, T.R. & PONCET, J. 1996. Status of southern elephant seals at South Georgia. *Antarctic Science* **8:** 237-244.

BRADSHAW, C.J.A., HINDELL, M.A., SUMNER, M.D. & MICHAEL, K.J. 2004. Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Animal Behaviour* **68:** 1349-1360.

BURTON, H.R. 1985. Tagging studies of male southern elephant seals (*Mirounga leonina* L.) in the Vestfold Hills area, Antarctica, and some aspects of their behaviour. In: *Studies of Sea Mammals in South Latitudes*, (ed) J.K. Ling & M.M. Bryden, pp. 19-30. Geographic Services (Pty) Ltd., Adelaide.

CAMERON, M.F. & SINIFF, D.B. 2004. Age-specific survival, abundance, and immigration rates of a Weddell seal (*Leptonychotes weddellii*) population in McMurdo Sound, Antarctica. *Canadian Journal of Zoology* **82:** 601-615.

CAMERON, M.F., SINIFF, D.B., PROFFITT, K.M. & GARROTT, R.A. 2007. Site fidelity of Weddell seals: the effects of sex and age. *Antarctic Science* **19:** 149-155.

CAMPAGNA, C. & LEWIS, M. 1992. Growth and distribution of a southern elephant seal colony. *Marine Mammal Science* **8:** 387-396.

CARRICK, R., CSORDAS, S.E. & INGHAM, S.E. 1962a. Studies on the southern elephant seal *Mirounga leonina* (L.). IV Breeding and development. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 161-197.

CARRICK, R., CSORDAS, S.E., INGHAM, S.E. & KEITH, K. 1962b. Studies on the southern elephant seal, *Mirounga leonina* (L.). III. The annual cycle in relation to age and sex. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 119-160.

CARRICK, R. & INGHAM, S.E. 1962a. Studies on the southern elephant seal, *Mirounga leonina* (L.) I. Introduction to the series. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 89-101.

CARRICK, R. & INGHAM, S.E. 1962b. Studies on the southern elephant seal, *Mirounga leonina* (L.) V. Population dynamics and utilization. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 198-206.

CAUGHLEY, G. 1977. *The analysis of vertebrate populations.* John Wiley, Chichester. 234 pp.

CHAUKE, L.F. 2009. Genetic variation and population structure of southern elephant seals *Mirounga leonina* from Marion Island. M.Sc., University of Pretoria, Pretoria.

CHILVERS, B.L. & WILKINSON, I.S. 2008. Philopatry and site fidelity of New Zealand sea lions (*Phocarctos hookeri*). *Wildlife Research* **35:** 463-470.

CLOBERT, J., DANCHIN, E., DHONDT, A. & NICHOLS, J.D. 2001. *Dispersal.* Oxford University Press, Oxford. 452 pp.

CONDY, P.R. 1979. Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.) at Marion Island. *South African Journal of Zoology* **14:** 95-102.

CROXALL, J.P. & HIBY, L. 1983. Fecundity, survival and site fidelity in the Weddell seals, *Leptonychotes weddelli*. *Journal of Applied Ecology* **20:** 19-32.

CUNNINGHAM, L., BAXTER, J.M., BOYD, I.L., DUCK, C.D., LONERGAN, M., MOSS, S.E. & MCCONNELL, B.J. 2009. Harbour seal movements and haul-out patterns: implications for monitoring and management. *Aquatic Conservation: Marine and Freshwater Ecosystems* **19:** 398-407.

DE BRUYN, M., HALL, B.L., CHAUKE, L.F., BARONI, C., KOCH, P.L. & HOELZEL, A.R. 2009. Rapid response of a marine mammal species to Holocene climate and habitat change. *PLoS Genetics* **5:** e1000554.

DE BRUYN, P.J.N. 2009. Life history studies of the southern elephant seal population at Marion Island. Ph.D., University of Pretoria, Pretoria.

DE BRUYN, P.J.N., TOSH, C.A., BESTER, M.N., CAMERON, E.Z., MCINTYRE, T. & WILKINSON, I.S. 2011. Sex at sea: alternative mating system in an extremely polygynous mammal. *Animal Behaviour* **82:** 445-451.

DE MOURA, J.F., DI DARIO, B.P.S., LIMA, L.M. & SICILIANO, S. 2010. Southern elephant seals (*Mirounga leonina*) along the Brazilian coast: review and additional records *Marine Biodiversity Records* **3:** e18.

DELONG, R.L., STEWART, B.S. & HILL, R.D. 1992. Documenting migrations of northern elephant seals using day length. *Marine Mammal Science* **8:** 155-159.

DINGLE, H. 1996. *Migration: the biology of life on the move.* Oxford University Press, Oxford. 474 pp.

DOBSON, F.S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour* **30:** 1183-1192.

FABIANI, A., GALIMBERTI, F., SANVITO, S. & HOELZEL, A.R. 2006. Relatedness and site fidelity at the southern elephant seal, *Mirounga leonina*, breeding colony in the Falkland Islands. *Animal Behaviour* **72:** 617-626.

FABIANI, A., HOELZEL, A.R., GALIMBERTI, F. & MUELBERT, M.M.C. 2003. Long-range paternal gene flow in the southern elephant seal. *Science* **299:** 676.

FORCADA, J. & ROBINSON, S.L. 2006. Population abundance, structure and turnover estimates for leopard seals during winter dispersal combining tagging and photo-identification data. *Polar Biology* **29:** 1052-1062.

GAINES, M.S. & MCCLENAGHAN, L.R. 1980. Dispersal in small mammals. *Annual Review of Ecology and Systematics* **11:** 163-196.

GALES, N.J., ADAMS, M. & BURTON, H.R. 1989. Genetic relatedness of two populations of the southern elephant seal, *Mirounga leonina*. *Marine Mammal Science* **5:** 57-67.

GALES, N.J. & BURTON, H.R. 1989. The past and present status of southern elephant seal (*Mirounga leonina* Linn.) in Greater Antarctica. *Mammalia* **53:** 35-48.

GALIMBERTI, F. & SANVITO, S. 1999. A very spatial relationship: GPS mapping aids understanding of elephant seal behaviour. *GPS World* **1999:** 22-28.

GENTRY, R.L. 1998. *Behavior and ecology of the northern fur seal.* Princeton University Press, Princeton. 392 pp.

GLEISS, A.C., JORGENSEN, S.J., LIEBSCH, N., SALA, J.E., NORMAN, B., HAYS, G.C., QUINTANA, F., GRUNDY, E., CAMPAGNA, C., TRITES, A.W., BLOCK, B.A. & WILSON, R.P. 2011. Convergent evolution in locomotory patterns of flying and swimming animals. *Nature Communications* **2:** 352.

GONZÁLEZ –SUÁREZ, M., FLATZ, R., AURIOLES-GAMBOA, D., HEDRICK, P.W. & GERBER, L.R. 2009. Isolation by distance among California sea lion populations in Mexico: redefining management stocks. *Molecular Ecology* **18:** 1088-1099.

GREENWOOD, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* **28:** 1140-1162.

GREENWOOD, P.J. & HARVEY, P.H. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* **13:** 1-21.

GREMMEN, N.J.M. 1981. The vegetation of the sub-Antarctic islands Marion and Prince Edward. *Geobotany* **3:** 149 pp.

GRIBEN, M.R. 1979. A study of the intermixture of subadult male fur seals *Callorhinus ursinus* (Linnaeus 1758) between the Pribilof Islands of St. George and St. Paul, Alaska. M.Sc., University of Washington, Seattle.

GUINET, C., JOUVENTIN, P. & WEIMERSKIRCH, H. 1992. Population changes, movements of southern elephant seals on Crozet and Kerguelen Archipelagos in the last decades. *Polar Biology* **12:** 349-356.

GUINET, C., JOUVENTIN, P. & WEIMERSKIRCH, H. 1999. Recent population changes of the southern elephant seal at Îles Crozet and Îles Kerguelen: the end of the decrease? *Antarctic Science* **11:** 193-197.

HALL, B.L., HOELZEL, A.R., BARONI, C., DENTON, G.H., LE BOEUF, B.J., OVERTURF, B. & TÖPF, A.L. 2006. Holocene elephant seal distribution implies warmer-than-present climate in the Ross Sea. *Proceedings of the National Academy of Sciences USA* **103:** 10213-10217.

HAMMILL, M.O. 1993. Seasonal movements of Hooded seals tagged in the Gulf of St. Lawrence, Canada. *Polar Biology* **13:** 307-310.

HARCOURT, R.G. 1992. Factors affecting early mortality in the South American fur seal (*Arctocephalus australis*) in Peru: density-related effects and predation. *Journal of Zoology, London* **226:** 259-270.

HARCOURT, R.G., KINGSTON, J.J., CAMERON, M.F., WAAS, J.R. & HINDELL, M.A. 2007. Paternity analysis shows experience, not age, enhances mating success in an aquatically mating pinniped, the Weddell seal (*Leptonychotes weddellii*). *Behavioural Ecology and Sociobiology* **61:** 643–652.

HEIMARK, R.J. & HEIMARK, G.M. 1986. Southern elephant seal pupping at Palmer Station, Antarctica. *Journal of Mammalogy* **67:** 189-190.

HIGGINS, L.V. & GASS, L. 1993. Birth to weaning: parturition, duration of lactation, and attendance cycles of Australian sea lions (*Neophoca cinerea*). *Canadian Journal of Zoology* **71:** 2047-2055.

HINDELL, M.A. & BURTON, H.R. 1988. The history of the elephant seal industry at Macquarie Island and an estimate of the pre-sealing numbers. *Papers and Proceedings of the Royal Society of Tasmania* **122:** 159-168.

HINDELL, M.A., HARCOURT, R., WAAS, J.R. & THOMPSON, D. 2002. Fine-scale three dimensional spatial use by diving, lactating female Weddell seals *Leptonychotes weddelli*. *Marine Ecology Progress Series* **242:** 275-284.

HINDELL, M.A. & LITTLE, G.J. 1988. Longevity, fertility and philopatry of two female southern elephant seals (*Mirounga leonina*) at Macquarie Island. *Marine Mammal Science* **4:** 168-171.

HINDELL, M.A. & MCMAHON, C.R. 2000. Long distance movement of a southern elephant seal (*Mirounga leonina*) from Macquarie Island to Peter 1 ØY. *Marine Mammal Science* **16:** 504-507.

HOELZEL, A.R., HALLEY, J., O'BRIEN, S.J., CAMPAGNA, C., ARNBOM, T., LE BOEUF, B.J., RALLS, K. & DOVER, G.A. 1993. Elephant seal genetic variation and the use of simulation models to investigate historical population bottlenecks. *Journal of Heredity* **84:** 443-449.

HOFFMAN, J.I., TRATHAN, P.N. & AMOS, W. 2006. Genetic tagging reveals extreme site fidelity in territorial male Antarctic fur seals *Arctocephalus gazella*. *Molecular Ecology* **15:** 3841-3847.

HOFMEYR, G.J.G. 2000. Dispersal and dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. M.Sc., University of Pretoria, Pretoria.

HOMER 1992. *The Odyssey (translated by T. E. Lawrence).* Wordsworth Classics, Ware, Hertfordshire, U.K. 210 pp.

HOWARD, W.E. 1960. Innate and environmental dispersal of individual vertebrates. *American Midland Naturalist* **63:** 152-161.

HUBER, H.R., ROVETTA, A.C., FRY, L.A. & JOHNSTON, S. 1991. Age-specific natality of northern elephant seals at the South Farallon Islands, California. *Journal of Mammalogy* **72:** 525-534.

INGHAM, S.E. 1957. Elephant seals on the Antarctic continent. *Nature* **180:** 1215-1216.

JESSOPP, M.J., FORCADA, J., REID, K., TRATHAN, P.N. & MURPHY, E.J. 2004. Winter dispersal of leopard seals (*Hydrurga leptonyx*): environmental factors influencing demographics and seasonal abundance. *Journal of Zoology, London* **263:** 251-258.

JOHNSON, D.W. 1990. A southern elephant seal (*Mirounga leonina* Linn.) in the northern hemisphere (Sultanate of Oman). *Marine Mammal Science* **6:** 242-243.

JONES, E. 1981. Age in relation to breeding status of the male southern elephant seal, *Mirounga leonina* (L.), at Macquarie Island. *Australian Wildlife Research* **8:** 327-334.

JONKER, F.C. & BESTER, M.N. 1998. Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island. *Antarctic Science* **10:** 21-30.

KELLY, B.P., BADAJOS, O.H., KUNNASRANTA, M., MORAN, J.R., MARTINEZ-BAKKER, M., WARTZOK, D. & BOVENG, P. 2010. Seasonal home ranges and fidelity to breeding sites among ringed seals. *Polar Biology* **33:** 1095-1109.

KENYON, K.W. 1960. Territorial behavior and homing in the Alaska fur seal. *Mammalia* **24:** 431-444.

KETTLEWELL, H.B.D. & RAND, B. 1955. Elephant seal cow and pup on South African coast. *Nature* **175:** 1000-1001.

KING, J.E. 1983. *Seals of the world.* Oxford University Press, Oxford. 240 pp.

KIRKMAN, S.P. 1999. The seasonal haulout cycle of the declining southern elephant seal, *Mirounga leonina*, population at Marion Island. M.Sc., University of Pretoria, Pretoria.

KIRKMAN, S.P., BESTER, M.N., HOFMEYR, G.J.G., JONKER, F.C., PISTORIUS, P.A., OWEN, R. & STRYDOM, N. 2004. Variation in the timing of the breeding haulout of female southern elephant seals at Marion Island. *Australian Journal of Zoology* **52:** 379-388.

KIRKMAN, S.P., BESTER, M.N., PISTORIUS, P.A., HOFMEYR, G.J.G., OWEN, R. & MECENERO, S. 2001a. Participation in the winter haulout by southern elephant seals (*Mirounga leonina*). *Antarctic Science* **13:** 380-384.

KIRKMAN, S.P., HOFMEYR, G.J.G., BESTER, M.N. & ISAKSEN, K. 2001b. Counts of southern elephant seals, *Mirounga leonina*, at Bouvet Island. *Polar Biology* **24:** 62-65.

KIYOTA, M. 2005. Site fidelity, territory acquisition and mating success in male northern fur seals (*Callorhinus ursinus*). *Mammal Study* **30:** 19-27.

KIYOTA, M., BABA, N. & MOURI, M. 1992. Occurrence of an elephant seal in Japan. *Marine Mammal Science* **8:** 433.

LAWS, R.M. 1954. The elephant seal (*Mirouga leonina* Linn.). I. Growth and age. *Falkland Islands Dependencies Survey Scientific Reports* **8:** 1-62.

LAWS, R.M. 1956. The elephant seal (*Mirounga leonina* Linn.). II. General social and reproductive behaviour. *Falkland Islands Dependencies Survey Scientific Reports* **13:** 1-88.

LAWS, R.M. 1960. The southern elephant seal (*Mirounga leonina*) at South Georgia. *Norsk Hvalfangst-Tidende* **49:** 466-476, 520-542.

LAWS, R.M. 1993. Identification of species. In: *Antarctic seals: research methods and techniques*, (ed) R.M. Laws, pp. 1-28. Cambridge University Press, Cambridge.

LE BOEUF, B.J., AINLEY, D.G. & LEWIS, T.J. 1974. Elephant seals on the Farallones: population structure of an incipient breeding colony. *Journal of Mammalogy* **55:** 370-385.

LE BOEUF, B.J. & LAWS, R.M. 1994. Elephant seals: an introduction to the genus. In: *Elephant seals: population ecology, behavior and physiology*, (ed) B.J. Le Boeuf & R.M. Laws, pp. 1-26. University of California Press, Berkeley.

LE ROUX, P.C. 2008. Climate and climate change. In: *The Prince Edward Islands: land-sea interactions in a changing ecosystem*, (ed) S.L. Chown & P.W. Froneman, pp. 39-64. SUNN PReSS, Stellenbosch.

LE ROUX, P.C. & MCGEOCH, M.A. 2008. Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Climatic Change* **86:** 309-329.

LEA, M.-A., JOHNSON, D., REAM, R., STERLING, J., MELIN, S. & GELATT, T. 2009. Extreme weather events influence dispersal of naive northern fur seals. *Biology Letters* **5:** 252-257.

LENGLART, P.Y. & BESTER, M.N. 1982. Post-weaning dispersion of southern elephant seal *Mirounga leonina* underyearlings at Kerguelen. *Revue d'Écologie (Terre et la Vie)* **36:** 175-186.

LESAGE, V., HAMMILL, M.O. & KOVACS, K.M. 2004. Long-distance movements of harbour seals (*Phoca vitulina*) from a seasonally ice-covered area, the St. Lawrence River estuary, Canada. *Canadian Journal of Zoology* **82:** 1070-1081.

LEWIS, M., CAMPAGNA, C. & QUINTANA, F. 1996. Site fidelity and dispersion of southern elephant seals from Patagonia. *Marine Mammal Science* **12:** 138-147.

LIDICKER, W.Z. & CALDWELL, R.L. 1982. *Dispersal and migration.* Hutchinson Ross, Stroudsburg, USA. 311 pp.

LING, J.K. & BRYDEN, M.M. 1992. *Mirounga leonina*. *Mammalian Species* **391:** 1-8.

LUNN, N.J. & BOYD, I.L. 1991. Pupping site fidelity of Antarctic fur seals at Bird Island, South Georgia. *Journal of Mammalogy* **72:** 202-206.

MANLEY, B., MCDONALD, L. & THOMAS, D. 1993. *Resource selection by animals. Statistical design and analysis for field studies.* Chapman and Hall, London. 221 pp.

MATTHIOPOULOS, J. 2003. The use of space by animals as a function of accessibility and preference. *Ecological Modelling* **159:** 239-268.

MATTHIOPOULOS, J., HARWOOD, J. & THOMAS, L. 2005. Metapopulation consequences of site fidelity for colonially breeding mammals and birds. *Journal of Animal Ecology* **74:** 716-727.

MCCANN, T.S. 1981. Aggression and sexual activity of male southern elephant seals, *Mirounga leonina*. *Journal of Zoology, London* **195:** 295-310.

MCCANN, T.S. 1985. Size, status and demography of southern elephant seal (*Mirounga leonina*) populations. In: *Studies of sea mammals at south latitudes*, (ed) J.K. Ling & M.M. Bryden, pp. 1-17. SouthAustralia Museum, Adelaide.

MCINTYRE, T., DE BRUYN, P.J.N., ANSORGE, I.J., BESTER, M.N., BORNEMANN, H., PLÖTZ, J. & TOSH, C.A. 2010. A lifetime at depth: vertical distribution of southern elephant seals in the water column. *Polar Biology* **33:** 1037-1048.

MCMAHON, C.R., BESTER, M.N., HINDELL, M.A., BROOK, B.W. & BRADSHAW, C.J.A. 2009. Shifting trends: detecting environmentally mediated regulation in long-lived marine vertebrates using time-series data. *Oecologia* **159:** 69-82.

MCMAHON, C.R. & CAMPBELL, D. 2000. Southern elephant seals breeding at Peterson Island Antarctica. *Polar Record* **36:** 51.

MÉLICE, J.-L., LUTJEHARMS, J.R.E., ROUAULT, M. & ANSORGE, I.J. 2003. Sea-surface temperatures at the sub-Antarctic islands Marion and Gough during the past 50 years. *South African Journal of Science* **99:** 363-366.

MILLS, J.A., RYDER, J.P., SHAW, P.W. & MCLAY, R. 1977. Further birth records of elephant seal *Mirounga leonina* in New Zealand (note). *New Zealand Journal of Marine and Freshwater Research* **11:** 789-791.

MOORE, J. & ALI, R. 1984. Are dispersal and inbreeding avoidance related? *Animal Behaviour* **32:** 94-112.

MORTON, M.L. 1992. Effects of sex and birth date on premigration biology, migration schedules, return rates and natal dispersal in the mountain white-crowned sparrow. *The Condor* **94:** 117-133.

MULAUDZI, T.W. 2005. Terrestrial haulout site usage by southern elephant seals, *Mirounga leonina*, at Marion Island. M.Sc. thesis, University of Pretoria, Pretoria.

MULAUDZI, T.W., HOFMEYR, G.J.G., BESTER, M.N., KIRKMAN, S.P., PISTORIUS, P.A., JONKER, F.C., MAKHADO, A.B., OWEN, J.H. & GRIMBEEK, R.J. 2008. Haulout site selection by southern elephant seals at Marion Island. *African Zoology* **43:** 25-33.

MUNYAI, F.M. 2006. Intersite movement by southern elephant seals ashore at Marion Island. M.Sc., University of Pretoria, Pretoria.

MURRAY, M.D. 1981. The breeding of the southern elephant seal, *Mirounga leonina* L, on the Antarctic continent. *Polar Record* **20:** 370-371.

NICHOLS, D.G. 1970. Dispersal and dispersion in relation to the birthsite of the southern elephant seal, *Mirounga leonina* (L.), of Macquarie Island *Mammalia* **34:** 598-616.

OOSTHUIZEN, W.C., BESTER, M.N., DE BRUYN, P.J.N. & HOFMEYR, G.J.G. 2009. Intra-archipelago moult dispersion of southern elephant seals at the Prince

Edward Islands, southern Indian Ocean. *African Journal of Marine Science* **31:** 457-462.

OOSTHUIZEN, W.C., BESTER, M.N., TOSH, C.A., GUINET, C., BESSON, D. & DE BRUYN, P.J.N. 2011. Dispersal and dispersion of southern elephant seals in the Kerguelen province, Southern Ocean. *Antarctic Science* **23:** 567-577.

OOSTHUIZEN, W.C., DE BRUYN, P.J.N., BESTER, M.N. & GIRONDOT, M. 2010. Cohort and tag-site-specific tag-loss rates in mark-recapture studies: a southern elephant seal cautionary case. *Marine Mammal Science* **26:** 350-369.

OOSTHUIZEN, W.H. 1991. General movements of South African (Cape) fur seals *Arctocephalus pusillus pusillus* from analysis of recoveries of tagged animals. *South African Journal of Marine Science* **11:** 21-29.

OOSTHUIZEN, W.H., DAVID, J.H.M. & ROSS, G.J.B. 1988. New records of southern elephant seals *Mirounga leonina* L. on the coast of southern Africa. *South African Journal of Marine Science* **7:** 75-86.

PANAGIS, K. 1981. Local movement of southern elephant seal pups *Mirounga leonina* (Linn.) at Marion Island. *South African Journal of Antarctic Research* **10/11:** 28-31.

PÄRT, T. 1991. Philopatry pays: a comparison between collared flycatcher sisters. *The American Naturalist* **138:** 790-796.

PÄRT, T. 1994. Male philopatry confers a mating advantage in the migratory collared flycatcher, *Ficedula albicollis*. *Animal Behaviour* **48:** 401-409.

PÄRT, T. 1995. Does breeding experience explain increased reproductive success with age? An experiment. *Proceedings of the Royal Society of London B* **260:** 113-117.

PEIMPWG (Prince Edward Islands Management Plan Working Group) 1996. *Prince Edward Islands Management Plan*. Department of Environmental Affairs and Tourism, Pretoria. 64 pp.

PETERSON, R.S., LE BOEUF, B.J. & DELONG, R.L. 1968. Fur seals from the Bering Sea breeding in California. *Nature* **219:** 899-901.

PINSKY, M.L., NEWSOME, S.D., DICKERSON, B.R., FANG, Y., VAN TUINEN, M., KENNETT, D.J., REAM, R.R. & HADLY, E.A. 2010. Dispersal provided resilience to range collapse in a marine mammal: insights from the past to inform conservation biology. *Molecular Ecology* **19:** 2418-2429.

PISTORIUS, P.A., BESTER, M.N., KIRKMAN, S.P. & TAYLOR, F.E. 2001. Temporal changes in fecundity and age at sexual maturity of southern elephant seals at Marion Island. *Polar Biology* **24:** 343-348.

PISTORIUS, P.A., KIRKMAN, S.P., BESTER, M.N. & TAYLOR, F.E. 2002. Implications of the winter haulout for future survival and resighting probablity of southern elephant seals at Marion Island. *South African Journal of Wildlife Research* **32:** 59-63.

POLAND, V.F., POMEROY, P.P., TWISS, S.D. & GRAVES, J.A. 2008. Fine-scale study finds limited evidence of kin clustering in a gray seal colony. *Marine Mammal Science* **24:** 371-387.

POMEROY, P.P., ANDERSON, S.S., TWISS, S.D. & MCCONNELL, B.J. 1994. Dispersion and site fidelity of breeding female grey seals (*Halichoerus grypus*) on North Rona, Scotland. *Journal of Zoology, London* **233:** 429-447.

POMEROY, P.P., REDMAN, P.R., RUDDELL, S.J.S., DUCK, C.D. & TWISS, S.D. 2005. Breeding site choice fails to explain interannual associations of female grey seals. *Behavioral Ecology and Sociobiology* **57:** 546-556.

POMEROY, P.P., TWISS, S.D. & DUCK, C.D. 2000a. Expansion of a grey seal (*Halichoerus grypus*) breeding colony: changes in pupping site use at the Isle of May, Scotland. *Journal of Zoology, London* **250:** 1-12.

POMEROY, P.P., TWISS, S.D. & REDMAN, P. 2000b. Philopatry, site fidelity and local kin associations within grey seal breeding colonies. *Ethology* **106:** 899-919.

RAND, R.W. 1959. The Cape fur seal (*Arctocephalus pusillus*): Distribution, abundance and feeding habits off the south western coast of the Cape Province. *Union of South Africa Department of Commerce Industries Division Fisheries Investigational Report* **No. 34:** 1-75.

REDMAN, P., POMEROY, P.P. & TWISS, S.D. 2001. Grey seal maternal attendance patterns are affected by water availability on North Rona, Scotland. *Canadian Journal of Zoology* **79:** 1073-1079.

REIDMAN, M. 1990. *The pinnipeds: seals, sealions and walruses.* University of California Press, Berkeley. 439 pp.

REISINGER, R.R. & BESTER, M.N. 2010. Long distance breeding dispersal of a southern elephant seal. *Polar Biology* **33:** 1289-1291.

REITER, J., PANKEN, K.J. & LE BOEUF, B.J. 1981. Female competition and reproductive success in northern elephant seals. *Animal Behaviour* **29:** 670-687.

RIDGWAY, S.H. & ROBISON, C.C. 1985. Homing by released captive California sea lions, *Zalophus californianus*, following release on distant islands. *Canadian Journal of Zoology* **63:** 2162-2164.

ROBERTSON, B.C., CHILVERS, B.L., DUIGNAN, P.J., WILKINSON, I.S. & GEMMELL, N.J. 2006. Dispersal of breeding, adult male *Phocarctos hookeri*:

Implications for disease transmission, population management and species recovery. *Biological Conservation* **127:** 227-236.

ROSS, G.J.B. 1969. The southern elephant seal on South African coasts. *Annals of the Cape Provincial Museums (Natural History)* **6:** 137-139.

SCAR-EGS 2011. Table 3. Estimated sizes and trends of southern elephant seal (*Mirounga leonina*) populations within the three stocks of the Southern Ocean. Scientific Committee for Antarctic Research - Expert Group on Seals. http://www.seals.scar.org/pdf/statusofstocs.pdf accessed 28 July 2011.

SCHAEFF, C.M., BONESS, D.J. & BOWEN, W.D. 1999. Female distribution, genetic relatedness, and fostering behaviour in harbour seals, *Phoca vitulina*. *Animal Behaviour* **57:** 427-434.

SCHMIDT-NIELSEN, K. 1972. Locomotion: energy cost of swimming, flying, and running. *Science* **177:** 222-228.

SCHULZE, B.R. 1971. The climate of Marion Island. In: *Marion and Prince Edward Islands: Report of the South African Biological & Geological Expedition/ 1965-1966*, (ed) E.M. Van Zinderen-Bakker, J.M. Winterbottom & R.A. Dyer, pp. 16-31. Balkema, Cape Town.

SETSAAS, T.H., BESTER, M.N., VAN NIEKERK, J.H., ROUX, J.-P. & HOFMEYR, G.J.G. 2008. Dispersion during the moult haulout of southern elephant seals at the Courbet Peninsula, Iles Kerguelen. *Polar Biology* **31:** 249-253.

SHIELDS, W.M. 1987. Dispersal and mating systems: investigating their causal connections. In: *Mammalian dispersal patterns: the effects of social structure on population genetics*, (ed) B.D. Chepko-Sade & Z.T. Halpin, pp. 3-24. University of Chicago Press, Chicago.

SLIP, D.J. & BURTON, H.R. 1999. Population status and seasonal haul-out patterns of the southern elephant seal (*Mirounga leonina*) at Heard Island. *Antarctic Science* **11:** 38-47.

SMITH, V.R. 1987. The environment and biota of Marion Island. *South African Journal of Science* **83:** 211-220.

SMITH, V.R. & STEENKAMP, M. 1990. Climatic change and its ecological implications at a sub-Antarctic island. *Oecologia* **85:** 14-24.

STEWART, B.S. 1989. The ecology and population biology of the northern elephant seal, *Mirounga leonina* Gill 1866, on the Southern California Channel Islands. Ph.D., University of California,

STEWART, B.S. & DELONG, R.L. 1992. Documenting migrations of northern elephant seals using day length. In: *Elephant seals: population ecology, behavior and physiology*, (ed) B.J. Le Boeuf & R.M. Laws, pp. 290-309. University of California Press, Berkeley.

STEWART, B.S., YOCHEM, P.K., HUBER, H.R., DELONG, R.L., JAMESON, R.J., SYDEMAN, W.J., ALLEN, S.G. & LE BOEUF, B.J. 1994. History and present status of the northern elephant seal population. In: *Elephant seals: population ecology, behavior and physiology*, (ed) B.J. Le Boeuf & R.M. Laws, pp. 29-48. University of California Press, Berkeley.

STIRLING, I. 1969. Ecology of the Weddell seal in McMurdo Sound, Antarctica. *Ecology* **50:** 573-586.

STIRLING, I. 1971. Studies on the behaviour of the south Australian fur seal, *Arctocephalus forsteri* (Lesson) II. Adult females and pups. *Australian Journal of Zoology* **19:** 267-273.

STIRLING, I. 1974. Movements of Weddell seals in McMurdo Sound, Antarctica. *Australian Journal of Zoology* **22:** 39-43.

STODDART, D.R. 1972. Pinnipeds or sirenians at western Indian Ocean Islands? *Journal of Zoology, London* **167:** 207-217.

T'HART, L., MOESKER, A., VEDDER, L. & VAN BREE, P.J.H. 1988. On the pupping period of grey seals, *Halichoerus grypus* (Fabricius, 1791), reproducing on a shoal near the Island of Terschelling, The Netherlands. *Zeitschrift für Säugetierkunde* **53:** 59-60.

TAYLOR, R.H. & TAYLOR, G.A. 1989. Re-assessment of the status of southern elephant seals (*Mirounga leonina*) in New Zealand. *New Zealand Journal of Marine and Freshwater Research* **23:** 201-213.

TESTA, J.W. 1987a. Juvenile survival and recruitment in a population of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. *Canadian Journal of Zoology* **65:** 2993-2997.

TESTA, J.W. 1987b. Long-term reproductive patterns and sighting bias in Weddell seals (*Leptonychotes weddellii*). *Canadian Journal of Zoology* **65:** 1091-1099.

THOMPSON, P.M. 1989. Seasonal changes in the distribution and composition of common seal (*Phoca vitulina*) haul-out groups. *Journal of Zoology, London* **217:** 281-294.

THOMPSON, P.M., KOVACS, K.M. & MCCONNELL, B.J. 1994a. Natal dispersal of harbour seals (*Phoca vitulina*) from breeding sites in Orkney, Scotland. *Journal of Zoology, London* **234:** 668-673.

THOMPSON, P.M. & MILLER, D. 1990. Summer foraging activity and movements of radio-tagged common seals (*Phoca vitulina* L.) in the Moray Firth, Scotland. *Journal of Applied Ecology* **27:** 492-501.

THOMPSON, P.M., MILLER, D., COOPER, R. & HAMMOND, P.S. 1994b. Changes in the distribution and activity of female harbour seals during the breeding season: implications for their lactation strategy and mating patterns. *Journal of Animal Ecology* **63:** 24-30.

TIERNEY, T.J. 1977. The southern elephant seal, *Mirounga leonina* (L.), in the Vestfold Hills, Antarctica. *Australian Wildlife Research* **4:** 13-24.

TWISS, S.D., POLAND, V.F., GRAVES, J.A. & POMEROY, P.P. 2006. Finding fathers: spatio-temporal analysis of paternity assignment in grey seals (*Halichoerus grypus*). *Molecular Ecology* **15:** 1939-1953.

TWISS, S.D., POMEROY, P.P. & ANDERSON, S.S. 1994. Dispersion and site fidelity of breeding male grey seals (*Halichoerus grypus*) on North Rona, Scotland. *Journal of Zoology, London* **233:** 683-693.

TWISS, S.D., WRIGHT, N.C., DUNSTONE, N., REDMAN, P., MOSS, S. & POMEROY, P.P. 2002. Behavioral evidence of thermal stress from overheating in U. K. breeding gray seals. *Marine Mammal Science* **18:** 455-468.

VAN DEN HOFF, J. 2001. Dispersal of southern elephant seals (*Mirounga leonina* L.) marked at Macquarie Island. *Wildlife Research* **28:** 413-418.

VAN DEN HOFF, J., BURTON, H.R. & RAYMOND, B. 2007. The population trend of southern elephant seals (*Mirounga leonina* L.) at Macquarie Island (1952–2004). *Polar Biology* **30:** 1275-1283.

VAN DEN HOFF, J., DAVIES, R. & BURTON, H.R. 2003. Origins, age composition and change in numbers of moulting southern elephant seals (*Mirounga leonina* L.) in the Windmill Islands, Vincennes Bay, east Antarctica, 1988-2001. *Wildlife Research* **30:** 275-280.

VAN PARIJS, S.M. & CLARK, C.W. 2006. Long-term mating tactics in an aquatic-mating pinniped, the bearded seal, *Erignathus barbatus*. *Animal Behaviour* **72:** 1269-1277.

VAUGHAN, R.W. 1967. South Georgia elephant seal found in South Africa. *British Antarctic Survey Bulletin* 90-91.

VERWOERD, W.J. 1971. Geology. In: *Marion and Prince Edward Islands: Report of the South African Biological & Geological Expedition/ 1965-1966*, (ed) E.M. Van Zinderen-Bakker, J.M. Winterbottom & R.A. Dyer, pp. 40-62. Balkema, Cape Town.

VINCENT, C., FEDAK, M.A., MCCONNELL, B.J., MEYNIER, L., SAINT-JEAN, C. & RIDOUX, V. 2005. Status and conservation of the grey seal, *Halichoerus grypus*, in France. *Biological Conservation* **126:** 62-73.

WACE, N.M. & HOLDGATE, M.W. 1976. Man and nature in the Tristan da Cunha Islands. *I.U.C.N. Monograph* **6:** 1-114.

WIIG, Ø. & ØIEN, N. 1987. Recoveries of grey seals *Halichoerus grypus* (Fabricius) tagged along the Norwegian coast. *Fauna Norgica Series A* **8:** 39-42.

WILKINSON, I.S. 1992. Factors affecting reproductive success of southern elephant seals, *Mirounga leonina*, at Marion Island. Ph.D., University of Pretoria, Pretoria.

WILKINSON, I.S. & BESTER, M.N. 1990. Duration of post-weaning fast and local dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. *Journal of Zoology, London* **222:** 591-600.

WILKINSON, I.S. & VAN AARDE, R.J. 1999. Marion Island elephant seal: the paucity-of-males hypothesis tested. *Canadian Journal of Zoology* **77:** 1547-1554.

WOLF, J.B.W. & TRILLMICH, F. 2007. Beyond habitat requirements: individual fine-scale site fidelity in a colony of the Galapagos sea lion (*Zalophus wollebaeki*) creates conditions for social structuring. *Oecologia* **152:** 553-567.

Chapter 2 ▪ History of movement and the dispersal of female southern elephant seals

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Does the history of terrestrial haulout site use by female southern elephant seals from Marion Island influence their choice of haulout sites?

Adult female southern elephant seal, Duiker's Point, Marion Island. Photo – G. Hofmeyr

"By the next afternoon the worst of the gale was over and we were able to get out and restock the larder. I went along the beach after skuas, as usual, and among a bunch of seal I spotted one about eighteen months old that had a brand mark on the back of its neck, a roman numeral. We had branded several hundred weaner pups the year before, hoping to find out whether the seal came back to their home beaches – this was the first that I had seen or heard of, and his number showed that he had come back to a beach at least in his own division."

L. Harrison Matthews (1952)

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History of movement and the dispersal of female southern elephant seals

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CHAPTER 2

HISTORY OF MOVEMENT AND THE DISPERSAL OF FEMALE SOUTHERN ELEPHANT SEALS

Abstract

Dispersal of animals has typically been related to natal site and the site of the first reproductive event (RH1), with animals showing significant fidelity to both of these sites. Where fidelity to other sites has been examined, it has seldom been compared to fidelity to the natal site or RH1 site, and never systematically. We examined the site fidelity of females of a migratory marine predator, the southern elephant seal *Mirounga leonina* to previous sites by systematically comparing fidelity to all sites visited during all four types of terrestrial periods experienced (natal, winter, moult and breeding) at different ages. This was made possible by a long-term mark-recapture programme that recorded the terrestrial behaviour of a number of cohorts of seals over the course of their lives. We found that female elephant seals showed significant fidelity to sites other than their natal site or RH1 site. Yearlings hauled out closest to their natal site, but older immature animals hauled out significantly closer to recently visited sites than to their natal site. At the first breeding event, however, seals hauled out closest to their natal site, but not significantly closer to this site than to a number of recently visited sites. Subsequently, as adults, they hauled out closest to the site at which the prior haulout event of the same type had taken place. Fidelity to sites other than the natal site possibly occurs during non breeding haulouts because of different requirements related to the physical and social environment of breeding and non-breeding sites. This is, however, not the case for the breeding haulout. It is possible that the temporal hiatus between birth and first breeding reduces the accuracy of return to the natal site, ensuring that animals return with greater fidelity to prior breeding sites, which are more familiar. Although one would expect elephant seals to show more fidelity to sites recently visited than to their natal site, because of greater familiarity to those sites, this is not always the case. Furthermore, the age at which breeding haulouts take place is also important, with older diparous and multiparous animals breeding significantly farther from their natal site. Familiarity with haulout sites is possibly only one of several cues used by seals in selecting a terrestrial haulout site, others including past experience at a site, the ease of navigation to a site and public information. This study is the first to systematically examine dispersal in relation to all sites used during one phase of an animal's life history over the course of its life.

Keywords: dispersal, site fidelity, habitat selection, southern elephant seal, *Mirounga leonina*

Introduction

Dispersal of animals has been related primarily to natal site and first breeding site (Greenwood 1980; Dobson 1982; Shields 1987; Clobert *et al.* 2001). These studies have shown that, while animals typically show fidelity to both of these sites, fidelity to the first breeding site is often greater (Greenwood 1980; Dobson 1982; Shields 1987). Fidelity to other sites has been considered far less often. Assessment of fidelity to non breeding sites, however, has included fidelity to moulting, winter and staging sites by migratory waterfowl (Anderson & Sterling 1974; Raveling 1979; Hestbeck *et al.* 1991;

Wilson *et al.* 1991; Bowman & Brown 1992; Warren *et al.* 1992; Bollinger & Derksen 1996; Reed *et al.* 1998; Robertson & Cooke 1999; Flint *et al.* 2000) and other species of migratory birds (Herzog & Keppie 1980; Harrington *et al.* 1988; Cantos & Telleria 1994; Merom *et al.* 2000; Wunderle & Latta 2000; Latta & Faaborg 2001; Cuandrado *et al.* 2008). Fidelity to foraging and winter areas has been shown for some species of marine mammals (Martin *et al.* 1984; Craig & Herman 1997; Salden *et al.* 1999; Goerlitz *et al.* 2003; Bradshaw *et al.* 2004; Acevedo *et al.* 2006; Valenzuela *et al.* 2009; Foote *et al.* 2010). None of these studies, however, has treated the dispersal of animals over the course of their lives in a systematic way and none has compared fidelity to natal, breeding and non breeding sites.

Here we report on a study that uses data provided by a long-term mark-recapture programme to systematically examining the dispersal of females of a migratory marine predator, the southern elephant seal *Mirounga leonina*, over the course of their lives within a prescribed study area. This has allowed us to determine which sites play a significant role in determining the choice of haulout site during subsequent haulouts.

Southern elephant seals are the largest of all pinnipeds (Laws 1993). They are primarily pelagic, inhabiting the waters of the Southern Ocean (Carrick & Ingham 1962; Ling & Bryden 1992; Wilkinson 1992). They undertake an annual double migration of thousands of kilometres between marine foraging grounds and isolated subantarctic islands, on which they haul out for brief terrestrial periods (Carrick *et al.* 1962a; Hindell & Burton 1988; Bester & Pansegrouw 1992; Wilkinson 1992; Jonker & Bester 1998). Over the course of their lives they may come ashore for four types of terrestrial periods. They are born ashore and spend some six-eight weeks ashore before and after weaning during the natal period. Throughout the course of their lives all elephant seals undertake an annual moult haulout. As an immature animal many elephant seals will undertake up to three winter haulouts per year. And finally, as an adult, they usually haul out annually during the breeding season (Laws 1956; Carrick *et al.* 1962a; Hindell & Burton 1988; Wilkinson 1992; Le Boeuf & Laws 1994), though individual animals skip occasional seasons (de Bruyn *et al.* 2011). These haulout periods are undertaken at specific times of the year by specific age classes (Carrick *et al.* 1962b; Condy 1979; Kirkman *et al.* 2003; Kirkman *et al.* 2004) and can be regarded as discrete events. Adult males reach maturity at an older age than females; at the study site 99 % are first recorded to breed from ages 6 – 9 (Mammal Research Institute unpublished data), while for females 97 % are first recorded to breed from ages 3 – 6 (de Bruyn 2009).

Like many other animals, southern elephant seals are philopatric, generally returning to their natal island during terrestrial haulouts (Carrick *et al.* 1962b; Carrick & Ingham 1962; Hindell & Little 1988; Campagna & Lewis 1992; Van den Hoff 2001; Fabiani *et al.* 2006). They do, however, infrequently move among islands within archipelago (Oosthuizen *et al.* 2009) and further a field (Vaughan 1967; Burton 1985; Bester 1988, 1989; Guinet *et al.* 1992; Hindell & McMahon 2000; Van den Hoff 2001; Reisinger & Bester 2010; Oosthuizen *et al.* 2011). Elephant seals also show significant fidelity to specific locations on their natal island or peninsula (Nichols 1970; Campagna & Lewis 1992; Hofmeyr 2000; Van den Hoff 2001; Fabiani *et al.* 2006). While they show fidelity to their natal site, they show greater fidelity to the site of their first reproductive haulout (RH1). Generally they show less fidelity to their natal site or their RH1 site when returning to moult or for the winter haulout than they do when returning to breed

(Hofmeyr 2000). Their fidelity to sites, within a prescribed study area, other than their natal and first reproductive haulout sites have not been examined systematically.

We examined the influence of history of haulouts on site selection by female southern elephant seals at Marion Island, Southern Ocean (46° 54' S., 37° 45' E.). We asked the following questions:

1. Do female southern elephant seals show fidelity to sites other than their natal or RH1 site?
2. Is this pattern the same for breeding, moult and winter haulouts?
3. Does the pattern of site fidelity change during the course of the animals' lives?

We applied this question to the most common pattern of life history among females, i.e. animals that are primiparous at the age of four. To account for a diversity of life histories we further asked:

4. Is this pattern affected by the age at which breeding events take place? That is, is it affected by the age of breeding onset and the age at which females return to breed?

Methods

Definition

For the purposes of this study we defined a site as a specific beach on an island, usually being less than one kilometre in length. Islands and island groups were noted as such and not as sites.

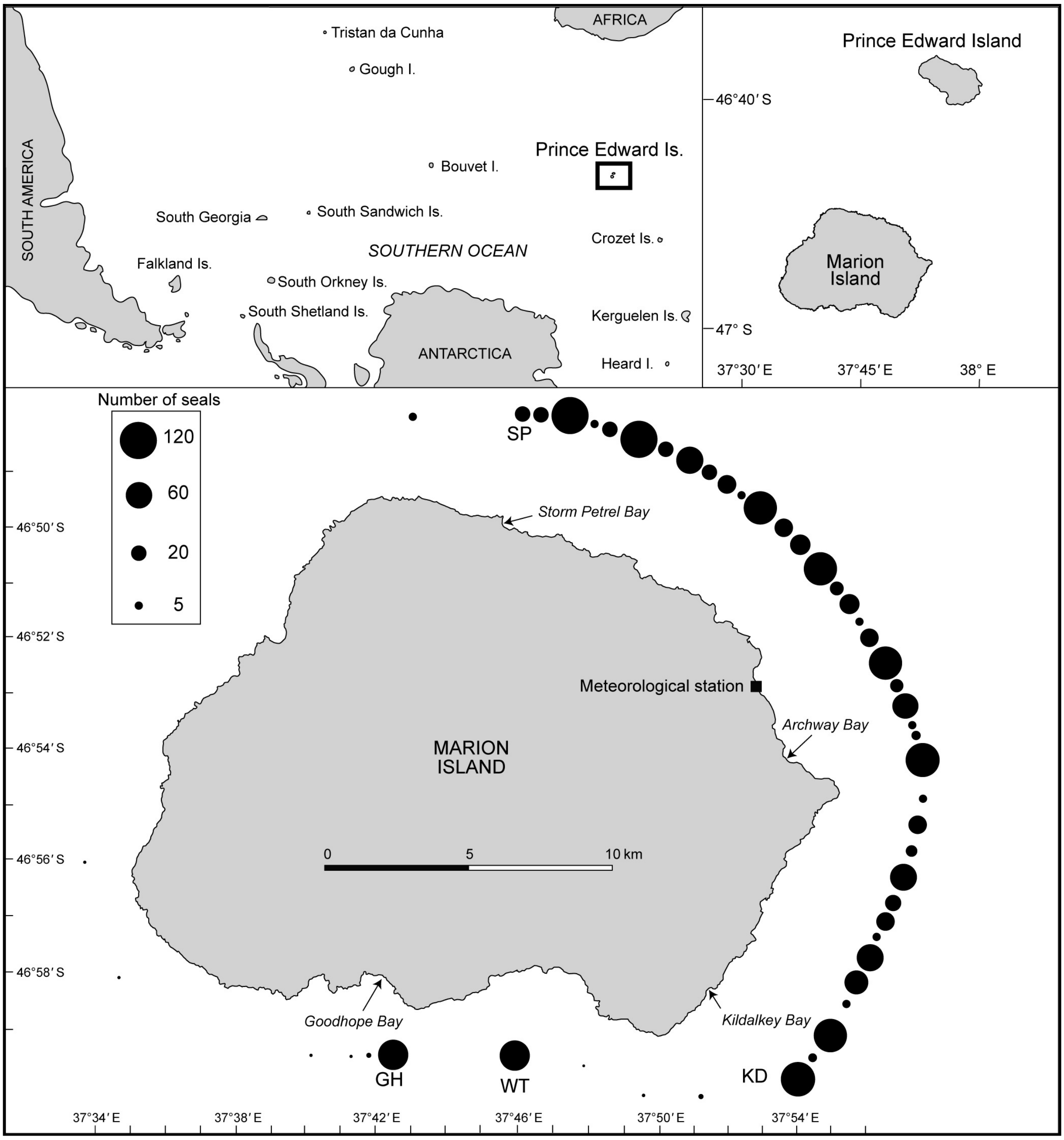

Figure 2.1 Map of Marion Island showing the distribution of southern elephant seals *Mirounga leonina*. The areas of the circles are directly proportional to the mean annual number of elephant seals hauling out at each site. The north and east sections of the coastline between locations marked SP and KD and at locations marked WT and GH form the study area. Reproduced from *African Journal of Marine Science* (2012) 34(3): 373-382 with permission © NISC (Pty) Ltd.

Study location

Marion Island is one of two islands in the Prince Edward Islands Archipelago. The island supports a population of approximately 2 100 elephant seals with some 500 pups born annually (Pistorius *et al.* 2004; Pistorius *et al.* 2011). These animals haul out in the Extended Study Area (ESA) on the north-east and east coasts, and part of the south coast of the island with some locations more popular than others (Figure 2.1). Southern elephant seals seldom come ashore outside of this area (Mulaudzi *et al.* 2008). All but two of the 40 beaches frequented by elephant seals in the ESA are separated from others by cliffs or other terrain generally impassable to elephant seals. Seals are therefore required to swim among most sites and the sites can be regarded as discrete entities.

Fieldwork

Data were collected from 1983 to 2003 as part of a long term monitoring programme. For this 9 963 southern elephant seals, representing all but a few of those born at the study site during the study period, were tagged at their natal site within days of weaning. Jumbo Rototags ® (produced by Dalton, Henley-on-Thames, UK) were applied to the interdigital webbing of both hind flippers of each seal. All seals received unique tags with a colour combination denoting cohort and a number denoting a specific individual within that cohort.

Tagged seals were resighted in the Extended Study Area. Systematic searches of this area for tagged seals took place at approximately regular intervals four times a month during the breeding season (mid August – late November) and three times a month outside of the breeding season. The greater number of searches during the breeding season allowed for an increased effort during that portion of the year when observing tags was perceived to be more difficult. The pattern of resights was further conducted as recorded in Table 2.1. During searches for elephant seals, tag colour and number was recorded in addition to location, behaviour and moult status. If possible, sex was checked to confirm that determined at tagging. Seals were assumed to age by one year on the 15th of October unless they had hauled out to breed, for which they were aged by a year from the beginning of the breeding season.

Table 2.1 The pattern of resight effort for tagged southern elephant seals *Mirounga leonina* in the Extended Study Area at Marion Island.

Month & Year (inclusive)	Sites and frequency of visits by observers	
	North-East & East Coast (sites MM051 – MM020)	South Coast (Sites MM025 & MM026)
Nov 1983 – May 1989	Every seven or ten days from Sep – May	Monthly from Sep – May
Aug 1989 – Aug 1992	Every seven or ten days throughout the year	Monthly throughout the year
Sep 1992 – Nov 2003	Every seven or ten days throughout the year	Every seven or ten days throughout the year

Data editing

The data for all cohorts were combined. Of the elephant seals tagged on Marion Island, 5023 were female. A total of 43 029 records of these animals were collected and were edited as follows:

1. Obvious errors were identified and either corrected or removed if they could not be corrected. This resulted in a database of 38 917 records. Obvious errors consisted of impossible data associations, for example female seals recorded as beachmasters, or recorded behaviour incompatible with a season, for example moulting animals recorded during the breeding season.
2. A single record was selected to represent each haulout event in each year by each seal and duplicates removed. The selected records were the first record at the location where the animal was sighted the most often during a particular haulout event. The following provisos were added: in the case of the breeding season, that the record selected be of a female accompanied by a pup, and during the annual moult, that the record be of a female actually moulting. Only for haulouts where the female was not recorded to be accompanied by a pup or where the seals was not actually moulting were other records considered. Where the number of records of sighting was equal for different locations, then the first record of the first location was selected. Records of additional winter haulouts during a year were also excluded since only 12.9 % of immature females returned for a second winter haulout. The resulting database consisted of 18 936 records.
3. Due to a reduced survival of seals with increasing age (Pistorius *et al.* 1999), the sample sizes of older animals participating in haulouts was relatively small. The database was therefore limited to animals of eight years or younger. This left 18 176 records for analysis.
4. Primiparous breeding females were selected as those being ashore for their first recorded breeding season aged 3 - 7 years inclusive (1127 records). Diparous breeding females had all been recorded ashore previously during a single breeding season and had began breeding before the age of seven (681 records). Multiparous

females had all been recorded ashore during two breeding seasons and had first bred before the age of seven (1079 records). Primiparity is assumed.

Splitting breeding animals into 3 groups (primiparous, diparous, multiparous) allowed us to look at the effect both of the location of RH1 site, and the location of other breeding sites. I.e. for diparous animals, we could compare fidelity to natal and RH1 sites, but for multiparous animals could compare fidelity to natal, RH1 site and prior breeding site. For multiparous animals this avoids having sites that are both RH1 sites and previous breeding sites.

Distances amongst all recorded haulouts for each seal were added to the database. These were determined as the shortest distance along the coastline from the centre of one site to another. Indentations along the coastline were ignored.

Due to the age limitation, a maximum possible total of 21 haulout or terrestrial events were noted for each individual: the natal period (N), winter haulouts from age zero to age two (W0 – W2), moult haulouts to age eight (M1 – M8), breeding haulouts from age three to age eight (B3 – B8), the previous breeding (PrB) and previous moult haulouts (PrM) and the haulouts of the first reproductive event (RH1). Few, if any of the seals were recorded during all of these haulout events.

Statistical Approach

The structure of the data for comparing two distances D_1 and D_2 (e.g. "*Distance from current haulout to natal site*" and "*Distance from current haulout to first winter site*", respectively) was schematically represented thus:

$$\begin{array}{cc} & \begin{array}{cc} D_1 & D_2 \end{array} \\ \mathbf{X} = & \begin{bmatrix} \mathbf{X}_{11} & \mathbf{0}_{12} \\ \mathbf{0}_{21} & \mathbf{X}_{22} \\ \mathbf{X}_{31} & \mathbf{X}_{32} \end{bmatrix} \end{array}$$

where $\mathbf{X}_{ij} : (n_{ij} \times 1)$ is a column vector of distances for n_{ij} individuals and $\mathbf{O}_{ij} : (n_{ij} \times 1)$ empty data vectors with no observations, with $(i = 1, 2, 3; \quad j = 1, 2)$. $\left[\text{Note: } n_{31} = n_{32}\right]$.

We considered different tests for comparing D_1 to D_2 e.g. a mixture of t-tests (paired and two-sample) or a mixture of nonparametric tests (e.g. Wilcoxon Signed Rank and Wilcoxon Rank Sum tests), because the data consists of both paired $\left(\mathbf{X}_{31} \text{ and } \mathbf{X}_{32}\right)$ and independent $\left(\mathbf{X}_{11} \text{ and } \mathbf{X}_{22}\right)$ data sets. However, because of difficulties in weighting of the components of these mixtures and complications in estimating the standard error, we decided to use the Jackknife approximation (Efron & Tibshirani 1998). This was done because the Jackknife can be considered as a near nonparametric test with the characteristic that it is an unbiased estimator of the arithmetic mean, and because the Jackknife, as proposed here, includes all available observations for a specific subset of the data e.g. Case III below.

The test statistic constructed for the general case is $T = a_{11}\overline{\mathbf{X}}_{11} + a_{22}\overline{\mathbf{X}}_{22} + a_{31}\overline{\mathbf{X}}_{31} + a_{32}\overline{\mathbf{X}}_{32}$, where $\overline{\mathbf{X}}_{ij}$ equals the arithmetic mean of the n_{ij} observations from $\mathbf{X}_{ij}$. The weights a_{ij} form a contrast such that $a_{11} + a_{22} + a_{31} + a_{32} = 0$. Due to incomplete data from a survey and that it was not gained by an experimental design, we identified the following cases (I to V) by which two distances D_1 and D_2 could be compared, namely:

Case I: $n_{11}, n_{22}, n_{31}, n_{32} > 0$, with a_{11}=-$a_{22} = a_{31} = -a_{32} = 1$

Case II: $n_{11}, n_{22} > 0, n_{31} = n_{32} = 0$, with a_{11}=-$a_{22} = 1, \quad a_{31} = a_{32} = 0$

Case III: $n_{11}, n_{31} = n_{32} > 0, n_{22} = 0$, with $2a_{11}$=$2a_{31}$=-$a_{32} = 1, \quad a_{22} = 0$

Case IV: $n_{22}, n_{31} = n_{32} > 0, n_{11} = 0$, with $-2a_{22}$=a_{31}=-$2a_{32} = 1, \quad a_{11} = 0$

Case V: $n_{31} = n_{32} > 0, \quad n_{11} = n_{22} = 0$, with a_{31}=-$a_{32} = 1, \quad a_{11} = a_{22} = 0$

Depending on the data structure (Cases I to V), Jackknife estimates

$$T_{JK(i)} = \left(a_{11}\overline{\mathbf{X}}_{11} + a_{22}\overline{\mathbf{X}}_{22} + a_{31}\overline{\mathbf{X}}_{31} + a_{32}\overline{\mathbf{X}}_{32}\right)_{(i)}, i = 1, \ldots, n$$

were obtained with the Jackknife estimator of

T given by $\overline{T}_{JK} = \frac{1}{n}\sum_{i=1}^{n} T_{JK(i)}$ and $SE_{JK} = \left\{\frac{n-1}{n}\sum_{i=1}^{n}\left(T_{JK(i)} - \overline{T}_{JK}\right)^2\right\}^{\frac{1}{2}}$

where $T_{JK(i)}$ is the estimator based on the complete dataset with observation i left out.

To construct CIs (confidence intervals) and hypothesis testing e.g. $\mu_{D_1} = \mu_{D_2}$ the assumption was made that $t_{JK} = \overline{T}_{JK} / SE_{JK}$ can be approximated by a t distribution with $(n-1)$ degrees of freedom.

For the data in question, we selected a subset and applied the chosen procedure. All differences were considered statistically significant on a 5% level of significance. Descriptive statistics of the raw data were provided to illustrate the results of the Jackknife. All analyses were completed using SAS (SAS.Institute.Inc. 2004)

Results

Site fidelity in relation to a history of haulouts – Moult

Moulting yearling female southern elephant seals did not haul out significantly closer to any one particular previously visited site (Figure 2.2a). Two-year-old moulters, however, hauled out significantly closer to their previous winter haulout site than to any other site, including their natal site (Figure 2.2b). Nulliparous three-year-old moulters, in contrast, hauled out significantly closer to their previous moult site than to any other site, also including their natal site (Figure 2.2c). Both parous four- and five-year-old moulters hauled out significantly closer to their previous moult site than to their natal site, than sites visited when a young immature animal and than all breeding sites. This site was, however, no closer than non-breeding haulouts visited recently (Figure 2.2d and 2.2e). Moulting six-year-olds, however, hauled out significantly closer to their previous moult site than to any other site except for their previous breeding haulout site (Figure 2.2f). The pattern shown by moulting seven- and eight-year-olds was similar, with females hauling out closest to their previous moult sites, but not significantly closer to this site than to other recent moult haulouts or their previous breeding haulout site. (Figure 2.2g and 2.2h).

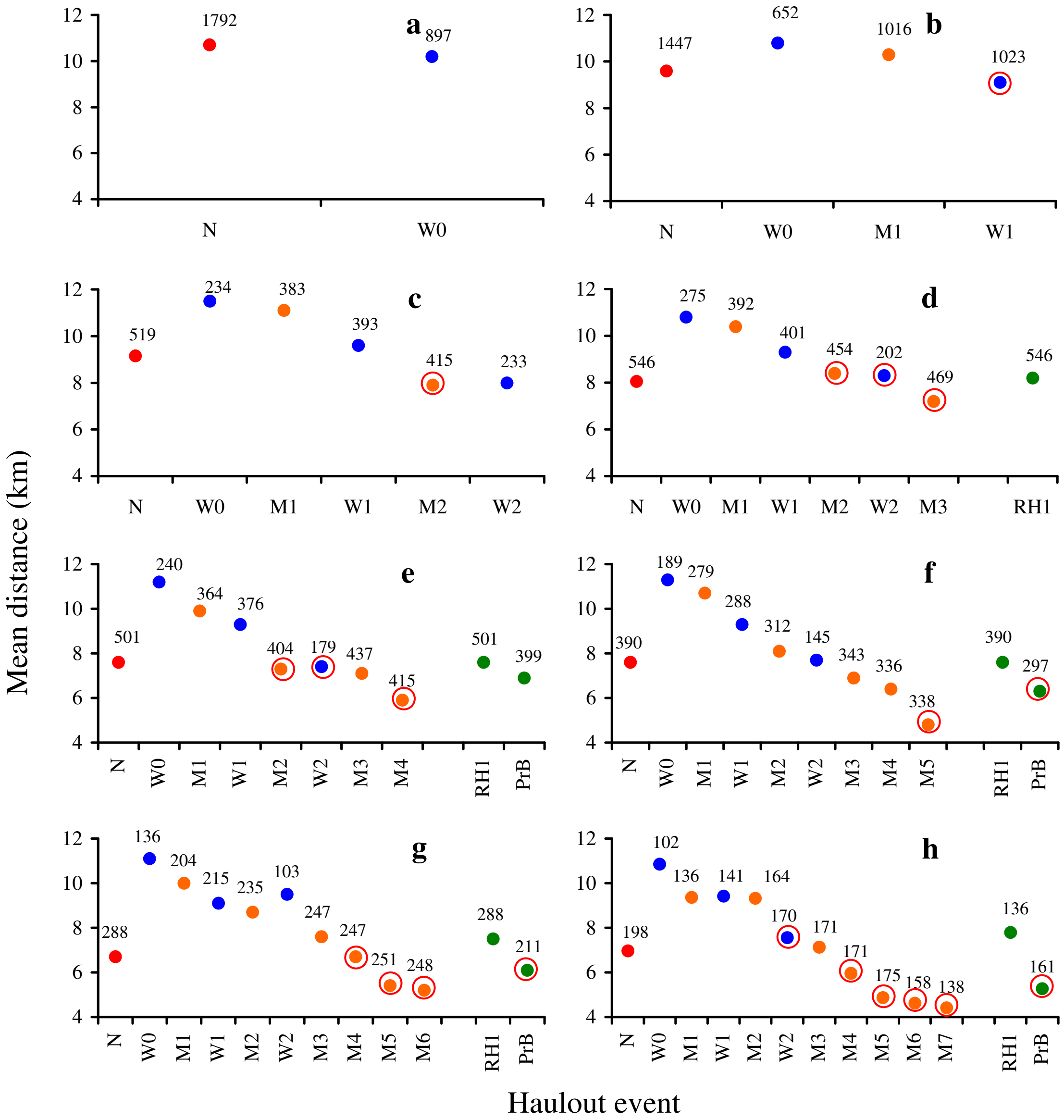

Figure 2.2 Mean distances between moult sites and various prior haulout sites, for female southern elephant seals *Mirounga leonina* of various ages at Marion Island. The ages are as follows: (a) yearling, (b) two-year-old, (c) three-year-old, (d) four-year-old, (e) five-year-old, (f) six-year-old, (g) seven-year-old, and (h) eight-year-old. Haulout sites are represented by: N – natal site, W0, W1 – winter haulout site visited as underyearlings, yearlings, etc respectively; M1, M2, etc – moult sites visited as yearlings, two-year-olds, etc respectively; RH1 – first breeding haulout site; PrB – previous breeding haulout site. Colours of points are coded as follows: red – natal event, blue – winter haulout, orange – moult haulout, and green – reproductive haulout. The numbers above the data points indicate sample sizes. Elephant seals have hauled out significantly closest to sites represented by circled data points.

Site fidelity in relation to a history of haulouts – Winter

When coming ashore for their winter haulout, yearling female southern elephant seals hauled out significantly closer to their natal site and previous haulout site (which is also their previous moult site) than to their previous winter haulout site (Figure 2.3a). At the age of two years, however, females coming ashore in winter hauled out closest to their previous winter haulout site, and significantly closer to that site than to any other site except for their previous moult haulout site (Figure 2.3b).

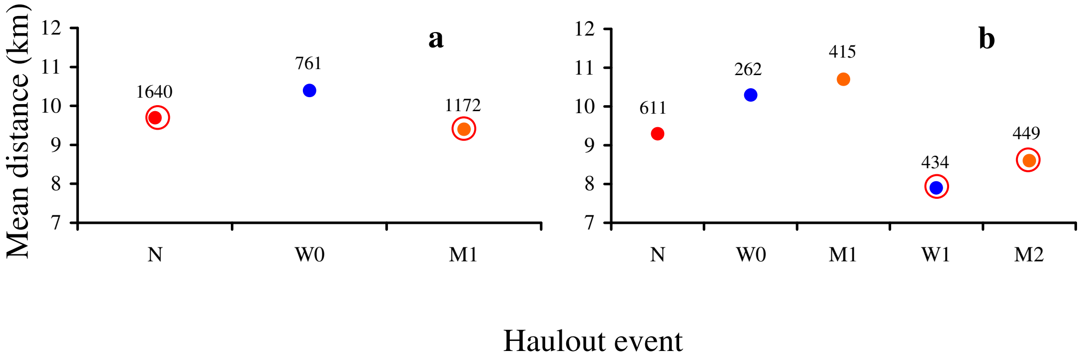

Figure 2.3 Mean distances between winter haulout sites as (a) yearlings or (b) two-year-olds, and various prior haulout sites, for female southern elephant seals *Mirounga leonina* at Marion Island. Haulout sites are represented by: N – natal site, W0, W1 – winter haulout site visited as underyearlings and yearlings respectively; M1, M2 – moult sites visited as yearlings and two-year-olds respectively. Colours of points are coded as follows: red – natal event, blue – winter haulout, and orange – moult haulout. The numbers above the data points are sample sizes. Elephant seals have hauled out significantly closest to sites represented by circled data points.

Site fidelity in relation to a history of haulouts – Breeding

Primiparous female southern elephant seals from Marion Island hauled out to breed closest to their natal site. While they hauled out significantly closer to this site than to sites visited when a young immature animal, this site was not significantly closer than recently visited sites (Figure 2.4a). When returning to breed for a second time, however, diparous female seals hauled out significantly closer to their RH1 site than to any other site visited previously except for their previous moult site. (Figure 2.4b). When returning to breed on subsequent occasions (third and greater reproductive events), multiparous female seals hauled out significantly closer to their previous breeding site than to any other site including their natal site, all sites visited as an immature animal, their previous moult site and their RH1 site (Figure 2.4c).

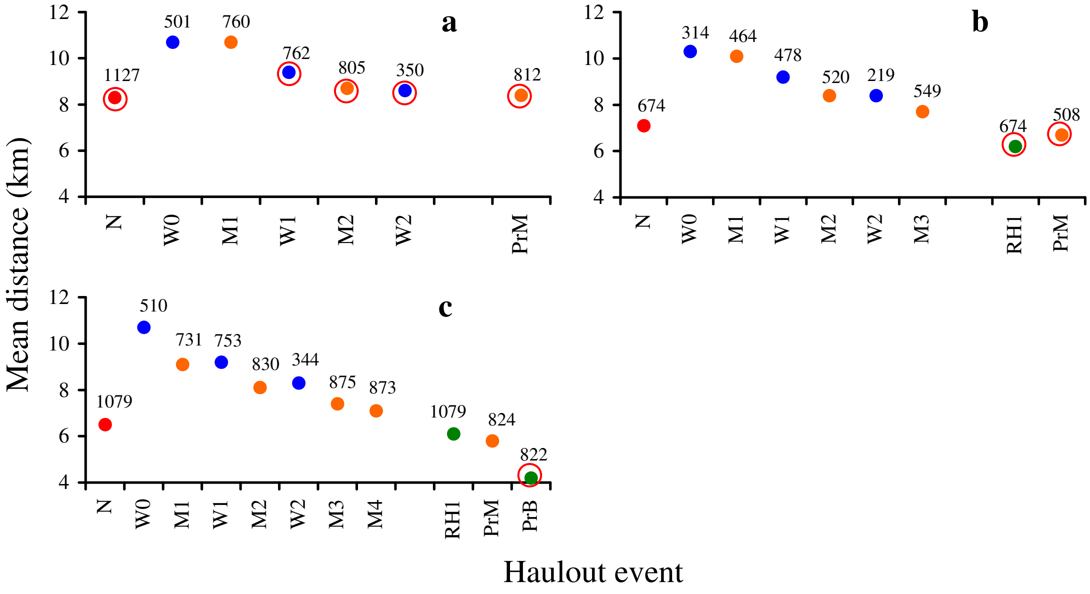

Figure 2.4 Mean distances between site of (a) primiparous, (b) diparous or (c) multiparous reproductive haulout event and various prior haulout sites, for female southern elephant seals *Mirounga leonina* at Marion Island. Haulout sites are represented by: N – natal site, W0, W1, etc – winter haulout site visited as underyearlings, yearlings, etc respectively; M1, M2, etc – moult sites visited as yearlings, two-year-olds, etc respectively; RH1 – first reproductive haulout site; PrM, PrB – moult site and breeding haulout site of the previous year respectively. Colours of points are coded as follows: red – natal event, blue – winter haulout, orange – moult haulout, and green – reproductive haulout. The numbers above the data points are sample sizes. The numbers above the data points are sample sizes. Elephant seals have hauled out significantly closest to sites represented by circled data points.

Site fidelity and the age of breeding haulouts – First reproductive haulout

Younger primiparous female southern elephant seals (three- and four-years-old) hauled out to breed closest to their natal site, but not significantly closer to this site than winter and moult sites visited recently (Figure 2.5a). The pattern for older primiparous female southern elephant seals (five- and six-years-old) was very similar but with the closest previous site being the previous moult site (Figure 2.5b).

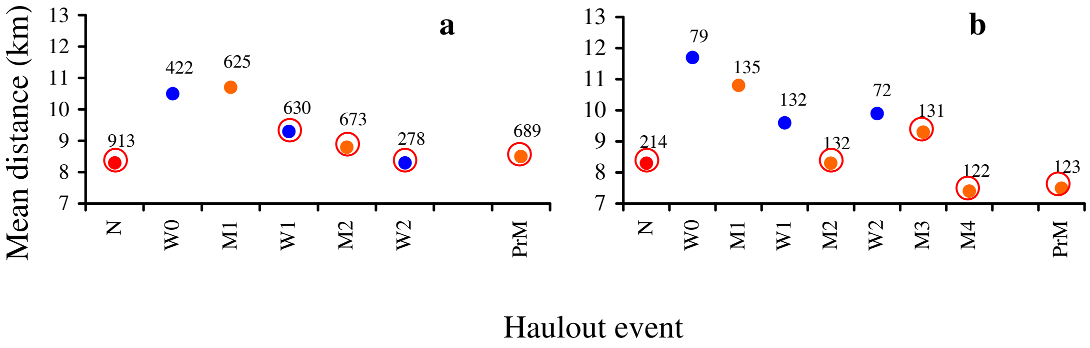

Figure 2.5 Mean distances between the sites of the first reproductive haulout event and various prior haulout sites, for (a) three- and four-year-old and (b) five-and six-year-old female southern elephant seals *Mirounga leonina* at Marion Island. Haulout sites are represented by: N – natal site, W0, W1, W2 – winter haulout site visited as underyearlings, yearlings and two-year-olds respectively; M1, M2, etc – moult sites visited as yearlings, two-year-olds, etc respectively; PrM – moult site of the previous year. Colours of points are coded as follows: red – natal event, blue – winter haulout, and orange – moult haulout. The numbers above the data points are sample sizes. Elephant seals have hauled out significantly closest to sites represented by circled data points.

Site fidelity and the age of breeding haulouts – Second reproductive haulout

Younger diparous females (four- and five-years-old) hauled out significantly closer to their RH1 site than to winter and moult haulout sites visited as immature animals, but hauled out no closer to their RH1 site than to their natal site or previous moult site (Figure 2.6a). The pattern of dispersal from previous haulout sites is similar for older diparous females (six- and seven-years-old), except that they hauled out significantly farther from their natal site than from their RH1 site or previous moult site (Figure 2.6b).

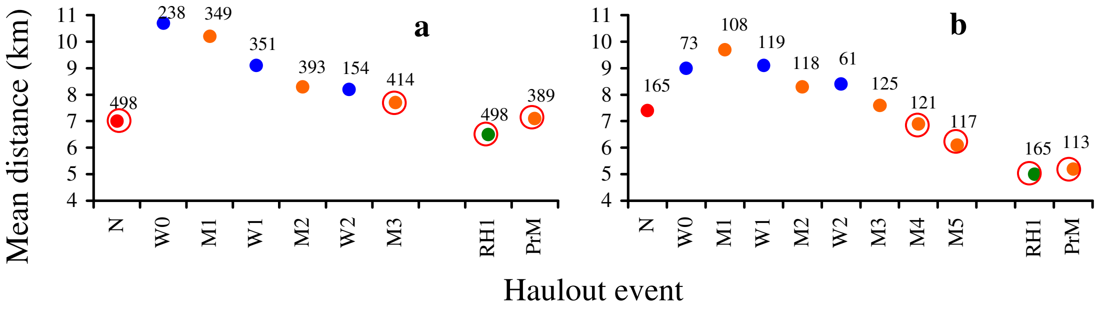

Figure 2.6 Mean distances between the sites of the second reproductive haulout event and various prior haulout sites, for (a) four- and five-year-old and (b) for six- and seven-year-old female southern elephant seals *Mirounga leonina* at Marion Island. Haulout sites are represented by: N – natal site, W0, W1, W2 – winter haulout site visited as underyearlings, yearlings and two-year-olds respectively; M1, M2, etc – moult sites visited as yearlings, two-year-olds, etc, RH1 – first reproductive haulout site, and PrM – moult site of the previous year. The numbers above the data points are sample sizes. Elephant seals have hauled out significantly closest to sites represented by circled data points.

Site fidelity and the age of breeding haulouts – Subsequent reproductive haulouts

Younger multiparous female southern elephant seals (five- and six-years-old) hauled out to breed significantly closer to their previous breeding site than to all sites visited as an immature animal and their first breeding site. They hauled out no closer to the previous breeding site, however, than to their natal site, and to one of their adult moult sites (Figure 2.7a). Older multiparous females (seven- and eight-years-old), by contrast hauled out significantly closer to their previous breeding site than to all sites previously visited, including their natal site (Figure 2.7b).

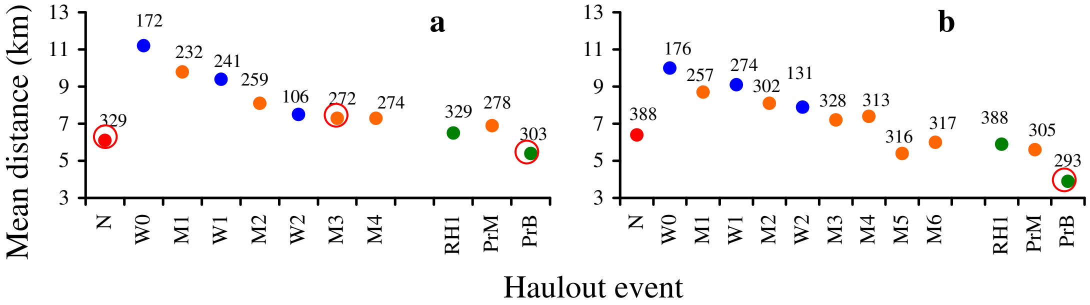

Figure 2.7 Mean distances between the sites of the third and greater reproductive haulout events and various prior haulout sites, for (a) five- and six-year-old and (b) for seven- and eight-year-old female southern elephant seals *Mirounga leonina* at Marion Island. Haulout sites are represented by: N – natal site; W0, W1, W2 – winter haulout site visited as underyearlings, yearlings and two-year-olds respectively; M1, M2, etc – moult sites visited as yearlings, two-year-olds, etc respectively; RH1,– first breeding haulout site and PrM , PrB – breeding haulout site and moult site of the previous year respectively. The numbers above the data points are sample sizes. Elephant seals have hauled out significantly closest to sites represented by circled data points.

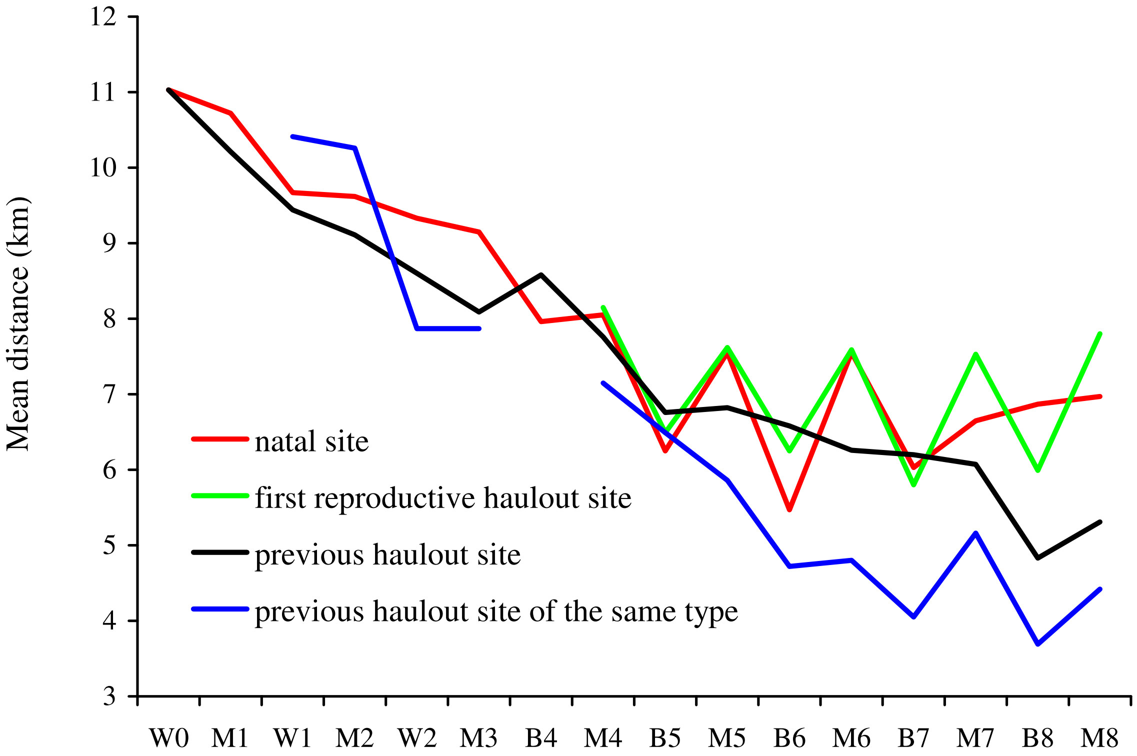

Figure 2.8 Mean distances between current haulout site and selected previous haulout sites by female southern elephant seals *Mirounga leonina* at Marion Island. Current haulout sites are represented by: N – natal site; W0, W1, W2 – winter haulout site visited as underyearlings, yearlings and two-year-olds respectively; M1, M2, etc – moult sites visited as yearlings, two-year-olds, etc respectively; B4, B5, etc – breeding sites visited as four-year-olds, five-year-olds, etc, respectively.

Table 2.2 Summary of effect of history of movement on choice of haulout site by female southern elephant seals *Mirounga leonina* at Marion Island. N – natal site, Im – moult and winter sites visited when immature, PrIm – haulout site visited as an immature animal on the previous haulout, M – sites visited when moulting, PrM – moult haulout site of the previous year, AdM - moult sites visited as an adult, RH1 – first breeding haulout site, PrB – breeding haulout site of the previous year.

	Current Haulout Event	Previous haulout sites close to the current haulout site	Previous haulout sites distant from the current haulout site
MOULTING	M1	N, Im	
	M2	PrIm	N, early Im
	M3 (have not bred)	PrM	N, early Im
	M4 (have bred)	recent Im, PrM	N, early Im, RH1
	M5 (have bred)	recent Im, PrM	N, early Im, RH1, PrB
	M6 (have bred)	PrM, PrB	N, Im, AdM, RH1
	M7 (have bred)	AdM, PrM, PrB	N, Im, RH1
	M8 (have bred)	AdM, PrM, PrB	N, Im, RH1
WINTER	W1	N, PrM	other Im
	W2	PrIm	N, other Im
BREEDING	RH1	N, recent Im, PrM	early Im
	RH2	PrM, RH1	N, Im
	RH>2	PrB	N, Im, AdM, PrM, RH1
	RH1 (younger)	N, recent Im, PrM	early Im
	RH1 (older)	N, recent Im, PrM	early Im
	RH2 (younger)	N, PrM, RH1	Im
	RH2 (older)	AdM, PrM, RH1	N, Im
	RH>2 (younger)	N, some AdM, PrB	Im, some AdM, PrM, RH1
	RH>2 (older)	PrB	N, Im, AdM, PrM, RH1

Discussion

In this study, we have described for the first time, the dispersal of an animal in relation to all previous sites visited, albeit only during one component of its life, the terrestrial phase. We have systematically compared distances displaced from a current site to all previous sites visited. The results show that the study animal displays significant fidelity to certain previously visited sites, in addition to their natal site and RH1 site. Furthermore they indicate that this varies with current behavioural state and age, and the history of terrestrial habitat use. The results also indicate the relevance of temporal discontinuity in site selection.

Female southern elephant seals at Marion Island follow a relatively simple pattern of dispersal in relation to their history of movement (Figure 2.8 and Table 2.2). As yearlings they haul out closest to their natal site and to their previous haulout site, but as older immature animals they haul out significantly closer to recent haulout sites only. This changes when they first haul out to breed; they then select a site closer to their natal site than to other sites. This site is, however, not significantly closer to their natal site than to a number of recently visited sites. When returning to breed for the second time, however, they haul out closer to their first breeding site than to any other site, though not significantly closer to this site than to their previous moult site. Subsequent haulouts as an adult follow a pattern of coming ashore closest to the site of the previous haulout of the same type, i.e. breeding closest to their previous breeding haulout site and moulting closest to their previous moult site. In the case of breeding haulouts, however, they haul out closest to the previous breeding site than any other. The level of fidelity shown by adult moulters is not as great.

This pattern of dispersal differs from that shown by studies that have only examined fidelity to natal site and first reproductive haulout site. Various authors have identified significant fidelity by elephant seals to both these locations (Carrick & Ingham 1962; Nichols 1970; Hindell & Little 1988; Campagna & Lewis 1992; Fabiani *et al.* 2006). This is also true for the population at the study site (Hofmeyr 2000), and for other species of seals (Testa 1987; Lunn & Boyd 1991; Pomeroy *et al.* 1994; Baker *et al.* 1995; Pomeroy *et al.* 2000; Karlsen *et al.* 2005). However, this study indicates that while female southern elephant seals do show fidelity to natal and RH1 sites, they show even greater fidelity to other previously visited sites except in the following situations. Greatest fidelity to their natal site is shown only when (1) they are yearlings and have visited very few sites other than their natal site, and (2) they haul out during their first breeding season. Greatest fidelity to their first breeding site is shown only when returning to breed as diparous animals. Thereafter they show greatest fidelity to the previous haulout site of the same type as the current haulout.

While a number of other studies have examined fidelity of southern elephant seals to previous haulout sites other than their natal or RH1 site (Carrick & Ingham 1962; Nichols 1970; Lenglart & Bester 1982; Hindell & Little 1988; Campagna & Lewis 1992; Lewis *et al.* 1996), these are generally of animals marked as adults. Their natal site and age is therefore unknown and a systematic comparison of changes in patterns of site fidelity cannot be determined. These animals also show fidelity to previous breeding sites, but whether these sites are first or later reproductive haulout sites are unknown.

Migratory animals are believed to attempt to return to their natal site to breed because their own survival is an indication that this is a suitable site at which to give birth and raise offspring to independence and to find mates (Pärt 1991; Morton 1992; Paradis *et al.* 1998). This factor will not be important when animals return for moult or winter haulouts and may explain the differences in fidelity seen when considering different types of haulouts. It is also quite possible that the topography of sites used by seals for the winter or moult is very different from those used during breeding (Stirling 1969; Nichols 1970; Huber *et al.* 1991; Hofmeyr 2000; Mulaudzi *et al.* 2008). Social requirements may also be different; the temporal overlap between the adult breeding season and the moult by immatures (Kirkman *et al.* 2003; Kirkman *et al.* 2004), and potentially high levels of harassment experienced during this time of the year (Galimberti *et al.* 2000c, a, b) may lead moulters to select sites away from breeding sites, and therefore potentially distant from their natal site (Hofmeyr 2000).

Elephant seals show similarities to the life histories of other migratory animals, such as waterfowl. Migratory waterfowl also show fidelity to breeding sites in addition to moult and winter sites (Bowman & Brown 1992; Bollinger & Derksen 1996; Reed *et al.* 1998; Robertson & Cooke 1999; Bêty *et al.* 2004). An important difference, however, is that the sites used for different purposes by waterfowl are separated spatially, often by many thousands of kilometres, whereas those used by elephant seals are usually (but not always, see Bester 1989; Huber *et al.* 1991; Oosthuizen *et al.* 2009; Oosthuizen *et al.* 2011) at a single island group or peninsula. This may complicate the assessment of fidelity to haulout sites used during different seasons, but it also potentially allows seals to use sites for more than just breeding or moulting. Visiting these sites may also allow seals to learn and thereby increase familiarity with a site. Southern elephant seals show some degree of fidelity to sites visited for purposes other than their current haulout, indicating that this is possibly a factor.

Pärt (1991; 1995) and Morton (1992) have both suggested that the temporal discontinuity between birth and the site of first reproduction may lead to a loss of familiarity with the natal site. The return of immature animals to their natal site may therefore assist them in maintaining familiarity with that site. This suggests that animals will return to sites that they have visited as immatures, rather than their natal site. The results suggest only a partial loss of familiarity with the natal site since seals hauled out to breed for the first time closest to their natal site and significantly closest to their natal site than to the sites visited as a young immature animal. The results also suggest, however, that the memory of recently visited sites may affect the accuracy of return to the natal site; they did not breed significantly closer to their natal site than to a number of recently visited sites.

When the age at which specific breeding haulouts take place is examined, important trends emerge in relation to the loss of familiarity with prior haulout sites. While seals showed no significant differences in relation to the age of primiparity, this was not the case for diparous and multiparous seals. For both categories, although there was no significant difference in the distance displaced from natal site than from first reproductive site in younger seals, older diparous and multiparous seals hauled out significantly closer to their first reproductive haulout site than to their natal site. A number of studies have indicated that various species of seals show an increase in site fidelity with age (Stirling 1974; Testa 1987; Huber *et al.* 1991; Reiter & Le Boeuf 1991; Baker *et al.* 1995). These studies have, however, examined the site fidelity of animals marked as adults. Should elephant seals at Marion Island show increased fidelity to a recently visited site with greater age, then it is logical that older animals will show significantly greater fidelity to these sites than to their natal site.

Conclusions

Ultimately, the memory of previous sites visited may be only one of a number of factors that determine which haulout site an animal selects. Factors related to experiences at past haulouts important, such as level of pup mortality, site popularity (and therefore the chance of finding suitable mates) or anthropogenic disturbance may also be important. Studies of other species of animals have shown that those which experience offspring mortality are more likely to breed at a different site in subsequent years (Bensch & Hasselquist 1991; Reed & Oring 1993; Aebischer 1995; Nager *et al.* 1996). Further, factors related to offshore topographical factors that may affect navigation close to a site may be important. Do certain features make specific sites easier to locate? Finally, public information, in the form of conspecific attraction or habitat copying, might also be important in determining a haulout site (Valone 1989, 2007). Animals sometimes use socially obtained cues such as the presence of conspecifics to make behavioural decisions in certain circumstances, including the selection of breeding sites (Podolsky 1990; Smith & Peacock 1990; Podolsky & Kress 1992; Reed & Dobson 1993; Jeffries & Brunton 2001). Conspecific attraction is known to influence habitat selection by migratory colonial seabirds (Danchin *et al.* 1998). It is possible that elephant seals do the same. Information garnered, by scent, sight or sound, on their approach to location may influence the haulout decisions of a female southern elephant seal. These questions are beyond the scope of this study, however, but are important to consider in the future.

Boyd (2002) stated that “The difficulties of tracking individuals through long time periods (on occasions for decades) and across large areas result in profound difficulties with the measurement of dispersal in marine predators. Consequently, virtually no study has been able to provide a comprehensive view of dispersal.” Here we have attempted to give a more comprehensive view of the dispersal of one marine predator, the southern elephant seal, at least as far as the terrestrial portion of its life is concerned. This has been made possible by the tracking of individual animals over more than two decades by the extensive application of plastic tags and great investment in resight effort. We have shown that female southern elephant seals show fidelity to specific sites dependant on their behavioural state and age. However, the terrestrial component is only one phase of their lives. Elephant seals spend the majority of their lives in the marine environment (McIntyre *et al.* 2010) exposed to a very different habitat. While the assessment of return to previous locations has been the subject of a number of studies (Bradshaw *et al.* 2004; Bailleul *et al.* 2007) further research will also be required here before a comprehensive picture of the site fidelity of this marine predator in both terrestrial and marine habitats emerges.

References

ACEVEDO, J., AGUAYO-LOBO, A. & PASTENE, L.A. 2006. Site fidelity of humpback whales (*Megaptera novaeangliae* Borowski, 1781) to the Magellan Strait feeding ground. *Revista de Biología Marina y Oceanografía* **41:** 11-19.

AEBISCHER, N.J. 1995. Philopatry and colony fidelity of shags *Phalacrocorax aristotelis* on the east coast of Britain. *Ibis* **137:** 11-18.

ANDERSON, D.R. & STERLING, R.T. 1974. Population dynamics of molting pintail drakes banded in south-central Saskatchewan. *Journal of Wildlife Management* **38:** 266-274.

BAILLEUL, F., CHARRASSIN, J.-B., MONESTIEZ, P., ROQUET, F., BIUW, M. & GUINET, C. 2007. Successful foraging zones of southern elephant seals from the Kerguelen Islands in relation to oceanographic conditions. *Philosophical Transactions of the Royal Society of London, B* **362:** 2169-2181.

BAKER, J.D., ANTONELIS, G.A., FOWLER, C.W. & YORK, A.E. 1995. Natal site fidelity in northern fur seals, *Callorhinus ursinus*. *Animal Behaviour* **50:** 237-247.

BENSCH, S. & HASSELQUIST, D. 1991. Territorial infidelity in the polygynous great reed warbler, *Acrocephalus arundinaceus*: the effect of variation in territory attractiveness. *Journal of Animal Ecology* **60:** 857-871.

BESTER, M.N. 1988. Marking and monitoring studies of the Kerguelen stock of southern elephant seals *Mirounga leonina* and their bearing on biological research in the Vestfold Hills. *Hydrobiologia* **165:** 269-277.

BESTER, M.N. 1989. Movements of southern elephant seals and Subantarctic fur seals in relation to Marion Island. *Marine Mammal Science* **5:** 257-265.

BESTER, M.N. & PANSEGROUW, H.M. 1992. Ranging behaviour of southern elephant seal cows from Marion Island. *South African Journal of Science* **88:** 574-575.

BÊTY, J., GIROUX, J.-F. & GAUTHIER, G. 2004. Individual variation in timing of migration:causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). *Behavioral Ecology and Sociobiology* **57:** 1-8.

BOLLINGER, K.S. & DERKSEN, D.V. 1996. Demographic characteristics of molting black brant near Teshekpuk Lake, Alaska. *Journal of Field Ornithology* **67:** 141-158.

BOWMAN, T.D. & BROWN, P.W. 1992. Site fidelity of male black ducks to a molting area in Labrador. *Journal of Field Ornithology* **63:** 32-34.

BOYD, I.L. 2002. The measurement of dispersal by seabirds and seals: implications for understanding their ecology. In: *Dispersal Ecology*, (ed) J.M. Bullock, R.E. Kenward & R.S. Hails, pp. 480. Cambridge University Press, Cambridge.

BRADSHAW, C.J.A., HINDELL, M.A., SUMNER, M.D. & MICHAEL, K.J. 2004. Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Animal Behaviour* **68:** 1349-1360.

BURTON, H.R. 1985. Tagging studies of male southern elephant seals (*Mirounga leonina* L.) in the Vestfold Hills area, Antarctica, and some aspects of their behaviour. In: *Studies of Sea Mammals in South Latitudes*, (ed) J.K. Ling & M.M. Bryden, pp. 19-30. Geographic Services (Pty) Ltd., Adelaide.

CAMPAGNA, C. & LEWIS, M. 1992. Growth and distribution of a southern elephant seal colony. *Marine Mammal Science* **8:** 387-396.

CANTOS, F.J. & TELLERIA, J.L. 1994. Stopover site fidelity of four migrant warblers in the Iberian Peninsula. *Journal of Avian Biology* **25:** 131-134.

CARRICK, R., CSORDAS, S.E., INGHAM, S.E. & KEITH, K. 1962a. Studies of the southern elephant seal, *Mirounga leonina* (L.). III. The annual cycle in relation to age and sex. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 119-160.

CARRICK, R., CSORDAS, S.E., INGHAM, S.E. & KEITH, K. 1962b. Studies on the southern elephant seal, *Mirounga leonina* (L.). III. The annual cycle in relation to age and sex. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 119-160.

CARRICK, R. & INGHAM, S.E. 1962. Studies on the southern elephant seal, *Mirounga leonina* (L.) I. Introduction to the series. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 89-101.

CLOBERT, J., DANCHIN, E., DHONDT, A. & NICHOLS, J.D. 2001. *Dispersal.* Oxford University Press, Oxford. 452 pp.

CONDY, P.R. 1979. Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.) at Marion Island. *South African Journal of Zoology* **14:** 95-102.

CRAIG, A.S. & HERMAN, L.M. 1997. Sex differences in site fidelity and migration of humpback whales (*Megaptera novaeangliae*) to the Hawaiian Islands. *Canadian Journal of Zoology* **75:** 1923-1933.

CUANDRADO, M., SENAR, J.C. & COPETE, J.L. 2008. Do all Blackcaps *Sylvia atricapilla* show winter site fidelity? *Ibis* **137:** 70-75.

DANCHIN, E., BOULINIER, T. & MASSOT, M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* **79:** 2415-2428.

DE BRUYN, P.J.N. 2009. Life history studies of the southern elephant seal population at Marion Island. Ph.D., University of Pretoria, Pretoria.

DE BRUYN, P.J.N., TOSH, C.A., BESTER, M.N., CAMERON, E.Z., MCINTYRE, T. & WILKINSON, I.S. 2011. Sex at sea: alternative mating system in an extremely polygynous mammal. *Animal Behaviour* **82:** 445-451.

DOBSON, F.S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour* **30:** 1183-1192.

EFRON, B. & TIBSHIRANI, R.J. 1998. *An introduction to the bootstrap.* Chapman and Hall / CRC Press, New York. 456 pp.

FABIANI, A., GALIMBERTI, F., SANVITO, S. & HOELZEL, A.R. 2006. Relatedness and site fidelity at the southern elephant seal, *Mirounga leonina*, breeding colony in the Falkland Islands. *Animal Behaviour* **72:** 617-626.

FLINT, P.L., PETERSEN, M.R., DAU, C.P., HINES, J.E. & NICHOLS, J.D. 2000. Annual survival and site fidelity of Steller's eiders molting along the Alaska peninsula. *The Journal of Wildlife Management* **64:** 261-268.

FOOTE, A.D., SIMILÄ, T., VÍKINGSSON, G.A. & STEVICK, P.T. 2010. Movement, site fidelity and connectivity in a top marine predator, the killer whale. *Evolution and Ecology* **24:** 803-814.

GALIMBERTI, F., BOITANI, L. & MARZETTI, I. 2000a. Female strategies of harassment reduction in southern elephant seals. *Ethology Ecology & Evolution* **12:** 367-388.

GALIMBERTI, F., BOITANI, L. & MARZETTI, I. 2000b. The frequency and costs of harassment in southern elephant seals. *Ethology Ecology & Evolution* **12:** 345-365.

GALIMBERTI, F., BOITANI, L. & MARZETTI, I. 2000c. Harassment during arrival on land and departure to sea in southern elephant seals. *Ethology Ecology & Evolution* **12:** 389-404.

GOERLITZ, D.S., URBÁN, J., ROJAS-BRACHO, L., BELSON, M. & SCHAEFF, C.M. 2003. Mitochondrial DNA variation among Eastern North Pacific gray whales (*Eschrichtius robustus*) on winter breeding grounds in Baja California. *Canadian Journal of Zoology* **81:** 1965-1972.

GREENWOOD, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* **28:** 1140-1162.

GUINET, C., JOUVENTIN, P. & WEIMERSKIRCH, H. 1992. Population changes, movements of southern elephant seals on Crozet and Kerguelen Archipelagos in the last decades. *Polar Biology* **12:** 349-356.

HARRINGTON, B.A., HAGAN, J.M. & LEDDY, L.E. 1988. Site fidelity and survival differences between two groups of new world red knots (*Calidris canutus*). *The Auk* **105:** 439-445.

HERZOG, P.W. & KEPPIE, D.M. 1980. Migration in a local population of spruce grouse. *The Condor* **82:** 366-372.

HESTBECK, J.B., NICHOLS, J.D. & MALECKI, R.A. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecology* **72:** 523-533.

HINDELL, M.A. & BURTON, H.R. 1988. The history of the elephant seal industry at Macquarie Island and an estimate of the pre-sealing numbers. *Papers and Proceedings of the Royal Society of Tasmania* **122:** 159-168.

HINDELL, M.A. & LITTLE, G.J. 1988. Longevity, fertility and philopatry of two female southern elephant seals (*Mirounga leonina*) at Macquarie Island. *Marine Mammal Science* **4:** 168-171.

HINDELL, M.A. & MCMAHON, C.R. 2000. Long distance movement of a southern elephant seal (*Mirounga leonina*) from Macquarie Island to Peter 1 ØY. *Marine Mammal Science* **16:** 504-507.

HOFMEYR, G.J.G. 2000. Dispersal and dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. M.Sc., University of Pretoria, Pretoria.

HUBER, H.R., ROVETTA, A.C., FRY, L.A. & JOHNSTON, S. 1991. Age-specific natality of northern elephant seals at the South Farallon Islands, California. *Journal of Mammalogy* **72:** 525-534.

JEFFRIES, D.S. & BRUNTON, D.H. 2001. Attracting endangered species to 'safe' habitats: responses of fairy terns to decoys. *Animal Conservation* **4:** 301-305.

JONKER, F.C. & BESTER, M.N. 1998. Seasonal movements and foraging areas of adult southern elephant seal, *Mirounga leonina*, females from Marion Island. *Antarctic Science* **10:** 21-30.

KARLSEN, O., HIBY, L., LUNDBERG, T., JÜSSI, M., JÜSSI, I. & HELANDER, B. 2005. Photo-identification, site fidelity, and movement of female gray seals (*Halichoerus grypus*) between haul-outs in the Baltic Sea. *Ambio* **34:** 628-634.

KIRKMAN, S.P., BESTER, M.N., HOFMEYR, G.J.G., JONKER, F.C., PISTORIUS, P.A., OWEN, R. & STRYDOM, N. 2004. Variation in the timing of the breeding haulout of female southern elephant seals at Marion Island. *Australian Journal of Zoology* **52:** 379-388.

KIRKMAN, S.P., BESTER, M.N., PISTORIUS, P.A., HOFMEYR, G.J.G., JONKER, F.C., OWEN, R. & STRYDOM, N. 2003. Variation in the timing of moult of southern elephant seals at Marion Island *South African Journal of Wildlife Research* **33:** 79-84.

LATTA, S.C. & FAABORG, J. 2001. Winter site fidelity of prairie warblers in the Dominican Republic. *The Condor* **103:** 455-468.

LAWS, R.M. 1956. The elephant seal (Mirounga leonina Linn.). II. General social and reproductive behaviour. *Falkland Islands Dependencies Survey Scientific Report* **13:** 1-88.

LAWS, R.M. 1993. Identification of species. In: *Antarctic seals: research methods and techniques*, (ed) R.M. Laws, pp. 1-28. Cambridge University Press, Cambridge.

LE BOEUF, B.J. & LAWS, R.M. 1994. Elephant seals: an introduction to the genus. In: *Elephant seals: population ecology, behaviour and physiology*, (ed) B.J. Le Boeuf & R.M. Laws, pp. 1-26. University of California Press, Berkeley.

LENGLART, P.Y. & BESTER, M.N. 1982. Post-weaning dispersion of southern elephant seal *Mirounga leonina* underyearlings at Kerguelen. *Revue d'Écologie (Terre et la Vie)* **36:** 175-186.

LEWIS, M., CAMPAGNA, C. & QUINTANA, F. 1996. Site fidelity and dispersion of southern elephant seals from Patagonia. *Marine Mammal Science* **12:** 138-147.

LING, J.K. & BRYDEN, M.M. 1992. *Mirounga leonina*. *Mammalian Species* **391:** 1-8.

LUNN, N.J. & BOYD, I.L. 1991. Pupping site fidelity of Antarctic fur seals at Bird Island, South Georgia. *Journal of Mammalogy* **72:** 202-206.

MARTIN, A.R., KATONA, S.K., MATILLA, D., HEMBREE, D. & WATERS, T.D. 1984. Migration of humpback whales between the Caribbean and Iceland. *Journal of Mammalogy* **65:** 330-333.

MATTHEWS, L.H. 1952. *Sea elephant: the life and death of the elephant seal.* MacGibbon and Kee, London. 190 pp.

MCINTYRE, T., DE BRUYN, P.J.N., ANSORGE, I.J., BESTER, M.N., BORNEMANN, H., PLÖTZ, J. & TOSH, C.A. 2010. A lifetime at depth: vertical distribution of southern elephant seals in the water column. *Polar Biology* **33:** 1037-1048.

MEROM, K., YOM-TOV, Y. & MCCLERY, R. 2000. Philopatry to stopover site and body condition of transient reed warblers during autumn migration through Israel. *The Condor* **102:** 441-444.

MORTON, M.L. 1992. Effects of sex and birth date on premigration biology, migration schedules, return rates and natal dispersal in the mountain white-crowned sparrow. *The Condor* **94:** 117-133.

MULAUDZI, T.W., HOFMEYR, G.J.G., BESTER, M.N., KIRKMAN, S.P., PISTORIUS, P.A., JONKER, F.C., MAKHADO, A.B., OWEN, J.H. & GRIMBEEK, R.J. 2008. Haulout site selection by southern elephant seals at Marion Island. *African Zoology* **43:** 25-33.

NAGER, R.G., JOHNSON, A.R., BOY, V., RENDON-MARTOS, M., CALDERON, J. & CÉZILLY, F. 1996. Temporal and spatial variation in dispersal in the greater flamingo (*Phoenicopterus ruber roseus*). *Oecologia* **107:** 204-211.

NICHOLS, D.G. 1970. Dispersal and dispersion in relation to the birthsite of the southern elephant seal, *Mirounga leonina* (L.), of Macquarie Island *Mammalia* **34:** 598-616.

OOSTHUIZEN, W.C., BESTER, M.N., DE BRUYN, P.J.N. & HOFMEYR, G.J.G. 2009. Intra-archipelago moult dispersion of southern elephant seals at the Prince Edward Islands, southern Indian Ocean. *African Journal of Marine Science* **31:** 457-462.

OOSTHUIZEN, W.C., BESTER, M.N., TOSH, C.A., GUINET, C., BESSON, D. & DE BRUYN, P.J.N. 2011. Dispersal and dispersion of southern elephant seals in the Kerguelen province, Southern Ocean. *Antarctic Science* **23:** 567-577.

PARADIS, E., BAILLIE, S.R., SUTHERLAND, W.J. & GREGORY, R.D. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* **67:** 518-536.

PÄRT, T. 1991. Philopatry pays: a comparison between collared flycatcher sisters. *The American Naturalist* **138:** 790-796.

PÄRT, T. 1995. Does breeding experience explain increased reproductive success with age? An experiment. *Proceedings of the Royal Society of London B* **260:** 113-117.

PISTORIUS, P.A., BESTER, M.N. & KIRKMAN, S.P. 1999. Survivorship of a declining population of southern elephant seals, *Mirounga leonina*, in relation to age, sex and cohort. *Oecologia* **121:** 201-211.

PISTORIUS, P.A., BESTER, M.N., LEWIS, M.N., TAYLOR, F.E., CAMPAGNA, C. & KIRKMAN, S.P. 2004. Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal (*Mirounga leonina*). *Journal of Zoology, London* **263:** 107-119.

PISTORIUS, P.A., DE BRUYN, P.J.N. & BESTER, M.N. 2011. Population dynamics of southern elephant seals: a synthesis of three decades of demographic research at Marion Island. *South African Journal of marine Science* **33:** 523-534.

PODOLSKY, R.H. 1990. Effectiveness of social stimuli in attracting Laysan albatross to new potential nesting sites. *The Auk* **107:** 119-124.

PODOLSKY, R.H. & KRESS, S.W. 1992. Attraction of the endangered dark-rumped petrel to recorded vocalizations in the Galápagos Islands. *The Condor* **94:** 448-453.

POMEROY, P.P., ANDERSON, S.S., TWISS, S.D. & MCCONNELL, B.J. 1994. Dispersion and site fidelity of breeding female grey seals (*Halichoerus grypus*) on North Rona, Scotland. *Journal of Zoology, London* **233:** 429-447.

POMEROY, P.P., TWISS, S.D. & REDMAN, P. 2000. Philopatry, site fidelity and local kin associations within grey seal breeding colonies. *Ethology* **106:** 899-919.

RAVELING, D.G. 1979. Traditional use of migration and winter roost sites by Canada geese. *The Journal of Wildlife Management* **43:** 229-235.

REED, E.T., COOCH, E.G., GOUDIE, R.I. & COOKE, F. 1998. Site fidelity of black brant wintering and spring staging in the Strait of Georgia, British Columbia. *The Condor* **100:** 426-437.

REED, J.M. & DOBSON, A.P. 1993. Behavioural constraints and conservation biology: conspecific attraction and recruitment. *Trends in Ecology and Evolution* **8:** 253-256.

REED, J.M. & ORING, L.W. 1993. Philopatry, site fidelity, dispersal, and survival of spotted sandpipers. *The Auk* **110:** 541-551.

REISINGER, R.R. & BESTER, M.N. 2010. Long distance breeding dispersal of a southern elephant seal. *Polar Biology* **33:** 1289-1291.

REITER, J. & LE BOEUF, B.J. 1991. Life history consequences of variation in age at primiparity in northern elephant seals. *Behavioral Ecology and Sociobiology* **28:** 153-160.

ROBERTSON, G.J. & COOKE, F. 1999. Winter philopatry in migratory waterfowl. *The Auk* **116:** 20-34.

SALDEN, D.R., HERMAN, L.M., YAMAGUCHI, M. & SATO, F. 1999. Multiple visits of individual humpback whales (*Megaptera novæangliæ*) between the Hawaiian and Japanese winter grounds. *Canadian Journal of Zoology* **77:** 504-508.

SAS.INSTITUTE.INC. 2004. *SAS/STAT 9.1 users guide.* SAS Institute Inc., Cary, N.C. pp.

SHIELDS, W.M. 1987. Dispersal and mating systems: investigating their causal connections. In: *Mammalian dispersal patterns: the effects of social structure on* *population genetics*, (ed) B.D. Chepko-Sade & Z.T. Halpin, pp. 3-24. University of Chicago Press, Chicago.

SMITH, A.T. & PEACOCK, M.M. 1990. Conspecific attraction and determination of metapopulation colonization rates. *Conservation Biology* **4:** 320-323.

STIRLING, I. 1969. Ecology of the Weddell seal in McMurdo Sound, Antarctica. *Ecology* **50:** 573-586.

STIRLING, I. 1974. Movements of Weddell seals in McMurdo Sound, Antarctica. *Australian Journal of Zoology* **22:** 39-43.

TESTA, J.W. 1987. Long-term reproductive patterns and sighting bias in Weddell seals (*Leptonychotes weddellii*). *Canadian Journal of Zoology* **65:** 1091-1099.

VALENZUELA, L.O., SIRONI, M., ROWNTREE, V.J. & SEGER, J. 2009. Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). *Molecular Ecology* **18:** 782-791.

VALONE, T.J. 1989. Group Foraging, Public Information, and Patch Estimation. *Oikos* **56:** 357-363.

VALONE, T.J. 2007. From eavesdropping on performance to copying the behavior of others: a review of public information use. *Behavioral Ecology and Sociobiology* **62:** 1-14.

VAN DEN HOFF, J. 2001. Dispersal of southern elephant seals (*Mirounga leonina* L.) marked at Macquarie Island. *Wildlife Research* **28:** 413-418.

VAUGHAN, R.W. 1967. South Georgia elephant seal found in South Africa. *British Antarctic Survey Bulletin* 90-91.

WARREN, S.M., WALSH, A.J., MERNE, O.J., WILSON, H.J. & FOX, A.D. 1992. Wintering site interchange amongst Greenland white-fronted geese *Anser* *albifrons flavirostris* captured at Wexford Slobs, Ireland. *Bird Study* **39:** 186-194.

WILKINSON, I.S. 1992. Factors affecting reproductive success of southern elephant seals, *Mirounga leonina*, at Marion Island. Ph.D., University of Pretoria, Pretoria.

WILSON, H.J., NORISS, D.W., WALSH, A., FOX, A.D. & STROUD, D.A. 1991. Winter site fidelity in Greenland white-fronted geese *Anser albifrons flavirostris*: implications for conservation and management. *Ardea* **79:** 287-294.

WUNDERLE, J.M. & LATTA, S.C. 2000. Winter site fidelity of Nearctic migrants in shade coffee plantations of different sizes in the Dominican Republic. *The Auk* **117:** 596-614.

Chapter 3 ▪ History of movement and the dispersal of male southern elephant seals

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Does the history of terrestrial haulout site influence the choice of haulout sites by male southern elephant seals at Marion Island? Is the pattern shown by males different to that shown by females?

Adult male southern elephant seal, Kildalkey Beach, Marion Island. Photo – G. Hofmeyr

“Fondness for company is one of the sea elephant's marked traits. An animal coming out of the sea is obviously not contented on a lonesome shore. It wanders about nervously between brief resting periods and soon returns to the water, perhaps feeling that it must find someone to quarrel with. A sea elephant when landing crawls slowly up the strand, stopping to let the waves break over it and taking advantage of every swell to aid its progress. When it has reached the upper beach it rises to its full height and reconnoiters; then, proceeding a little further it repeats the action, or if it spies none of its kind it may take a siesta before continuing the search.”

Robert Cushman Murphy (1914)

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History of movement and the dispersal of male southern elephant seals

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CHAPTER 3

HISTORY OF MOVEMENT AND THE DISPERSAL OF MALE SOUTHERN ELEPHANT SEALS

Abstract

Studies of dispersal have noted significant fidelity to their natal site and the site of first reproduction in many species of mammals and birds. Many of these studies have also noted a sex bias in dispersal and site fidelity. The patterns revealed have been used to explain why dispersal takes place. Few studies have, however, considered fidelity to non breeding sites, or sex bias in fidelity to non breeding sites, and none have investigated the patterns of sex bias in site fidelity shown by animals over the entire course of their lives, possibly leading to an incomplete view of dispersal. We attempted to counter this by systematically assessing fidelity to natal, winter, moult and breeding sites, during the terrestrial phase of their lives, by males of a migratory marine predator. We then compared the patterns shown to those of females. This study used data generated by a long term mark-recapture programme of the population of southern elephant seals *Mirounga leonina* at Marion Island, Southern Ocean. The patterns of dispersal shown by male elephant seals changed over the course of their lives, depending on their age and behavioural state. While they show significant fidelity to their natal site, they haul out significantly closer to certain other sites visited during the course of their lives, than to their natal site. As immature animals, they hauled out closest to their natal site, but no closer to this site than to recently visited sites. Once they had reached maturity, however, and including their first breeding event, they hauled out significantly closer to recently visited sites than to their natal site. This pattern differs to that of females, which hauled out closer to recently visited sites than to their natal site as immatures, but show an increase in fidelity to their natal site at their first breeding event. Differences in the dispersal of male and female pinnipeds is to be expected in the light of the great intersexual differences in behaviour and life history showed by this taxon.

Keywords: dispersal, site fidelity, habitat selection, sex bias, southern elephant seal, *Mirounga leonina*

Introduction

Sex bias in site fidelity is typical of both birds and mammals (Greenwood 1980; Dobson 1982). Patterns of sex bias have been characterised by reference to life history in an attempt to explain why animals disperse. Greenwood (1980) suggested that the social system determines the predominantly dispersing sex. He noted that females are the dispersing sex in most monogamous species and species showing resource defence polygyny whereas males are the dispersing sex in most species showing mate defence polygyny. These patterns have been interpreted in the light of advantages that might accrue to the sex that defends resources from familiarity with a previously visited site (Greenwood 1980; Dobson 1982).

Studies of dispersal have generally considered fidelity to the natal site and the site of the first reproductive event only. Animals typically show significant fidelity to both of these sites (Greenwood 1980; Dobson 1982; Shields 1987; Clobert *et al.* 2001), but often greater fidelity to the site of the first reproductive event (Greenwood 1980; Dobson

1982; Shields 1987). Studies that have considered fidelity to other sites, primarily examined the return of migrants to moult, winter and staging sites (Metcalfe & Furness 1985; Hestbeck *et al.* 1991; Cantos & Telleria 1994; Reed *et al.* 1998; Robertson & Cooke 1999; Hamer *et al.* 2001; Foote *et al.* 2010). However, none of these studies compared fidelity to non breeding sites and fidelity to breeding sites (see Chapter 2). And few studies considered sex bias in fidelity to non breeding sites (Robertson & Cooke 1999). Ignoring these two aspects may have important behavioural and demographic consequences (Robertson & Cooke 1999). We attempted to counter this in this study by a systematic examination of the terrestrial aspects of the dispersal of male southern elephant seals *Mirounga leonina* over the course of their lives, as we did for females (see Chapter 2) and by a comparison of the patterns shown by the two sexes.

Southern elephant seals are the largest of all pinnipeds with adult males reaching masses of 1.5 – 3 tons (Ling & Bryden 1992). Adult females are considerably smaller, generally being 350 – 800 kilograms in mass (Fedak et al. 1994). At the study site, adult females begin breeding at ages three to six (de Bruyn 2009), whereas males begin breeding at ages six to nine (Mammal Research Institute unpublished data). They inhabit the Southern Ocean, and are primarily pelagic (McIntyre *et al.* 2010a). Southern elephant seals undertake double annual migrations of several thousand kilometres each between pelagic foraging areas and terrestrial haulouts on isolated subantarctic islands (Carrick *et al.* 1962b; Hindell & Little 1988; Bester & Pansegrouw 1992; Wilkinson 1992; Jonker & Bester 1998). Terrestrial periods ashore are brief, seasonal and loosely synchronised (Kirkman et al. 2003; Kirkman et al. 2004). These periods are characterised by an absence from the sea for all except brief immersions in the shallows (Condy 1979; Wilkinson & Bester 1990) and rare movements among adjacent sites

(Munyai 2006) and therefore each can be regarded as a naturally discrete event. Four types of terrestrial periods are experienced over the course of an elephant seals life: the natal period, and the winter, moult and breeding haulouts. Elephant seals are born during the natal period, following which they spend three weeks ashore pre-weaning and up to five weeks post weaning (Laws 1956; Carrick *et al.* 1962b; Condy 1979). Immature elephant seals are recorded ashore in most years during the autumn and winter for periods of several weeks (Kirkman *et al.* 2001; Pistorius *et al.* 2002). All elephant seals undertake an annual moult haulout in the spring or summer throughout their lives (Condy 1979; Kirkman *et al.* 2003). And finally, during the spring adult elephant seals haul out during most years to breed (Condy 1979; Kirkman *et al.* 2004). Adult females come ashore for a month during this period, during which time they give birth, suckle their pups to weaning, and mate. Adult males haul out during the breeding season for periods of several weeks to three months during which they compete for control of aggregations of females, attempt to defend these aggregations and mate (Laws 1956; Carrick *et al.* 1962a; Hindell & Burton 1988; Wilkinson 1992; Le Boeuf & Laws 1994; Kirkman *et al.* 2003; Kirkman *et al.* 2004).

The aims of this study were to answer a number of questions in relation to site fidelity and past history of movement: (1) Do male southern elephant seals show fidelity to any sites other than their natal site or site of the first reproductive event? (2) Does this pattern differ according to the type of haulout? (3) Does the pattern change over the course of the seals’ lives? We then further asked (4) does the pattern of dispersal shown by males differ to that described for females?

Methods

Definition

A site is defined as a specific beach on an island, usually of less than one kilometre in length. The word “site” is not used in relation to broader geographic locations, such as islands or island groups.

Study location

Data were collected from the population of southern elephant seals at isolated subantarctic Marion Island (Figure 3.1). This is one of two islands in the Prince Edward Islands Archipelago (46º 54' S., 37º 45' E.). Population size is estimated at 2100 seals of all age classes, with a pup production figure of approximately 500 (Pistorius *et al.* 2004; Pistorius *et al.* 2011). Elephant seals haul out primarily on the north east, east and parts of the south coast in a section known as the Extended Study Area (ESA). Outside of this area the terrain is unsuitable for them (Wilkinson 1992) and negligible numbers of seals are recorded (Mulaudzi *et al.* 2008). Some of the 40 locations within the ESA are more popular than others. These sites are separated from each other in all but two instances, by terrain impassable to elephant seals. Since seals are required to swim before they move among sites, each can be regarded as a naturally discrete spatial entity.

Fieldwork

An ongoing long-term mark-recapture programme generated the data analysed in this study. From 1983 to 2003, almost all elephant seal pups of 21 cohorts (9 963 animals) were marked in the study area. These were tagged at their natal site shortly after weaning. A Jumbo Rototag ® (Dalton, Henley-on-Thames, UK) was applied to the

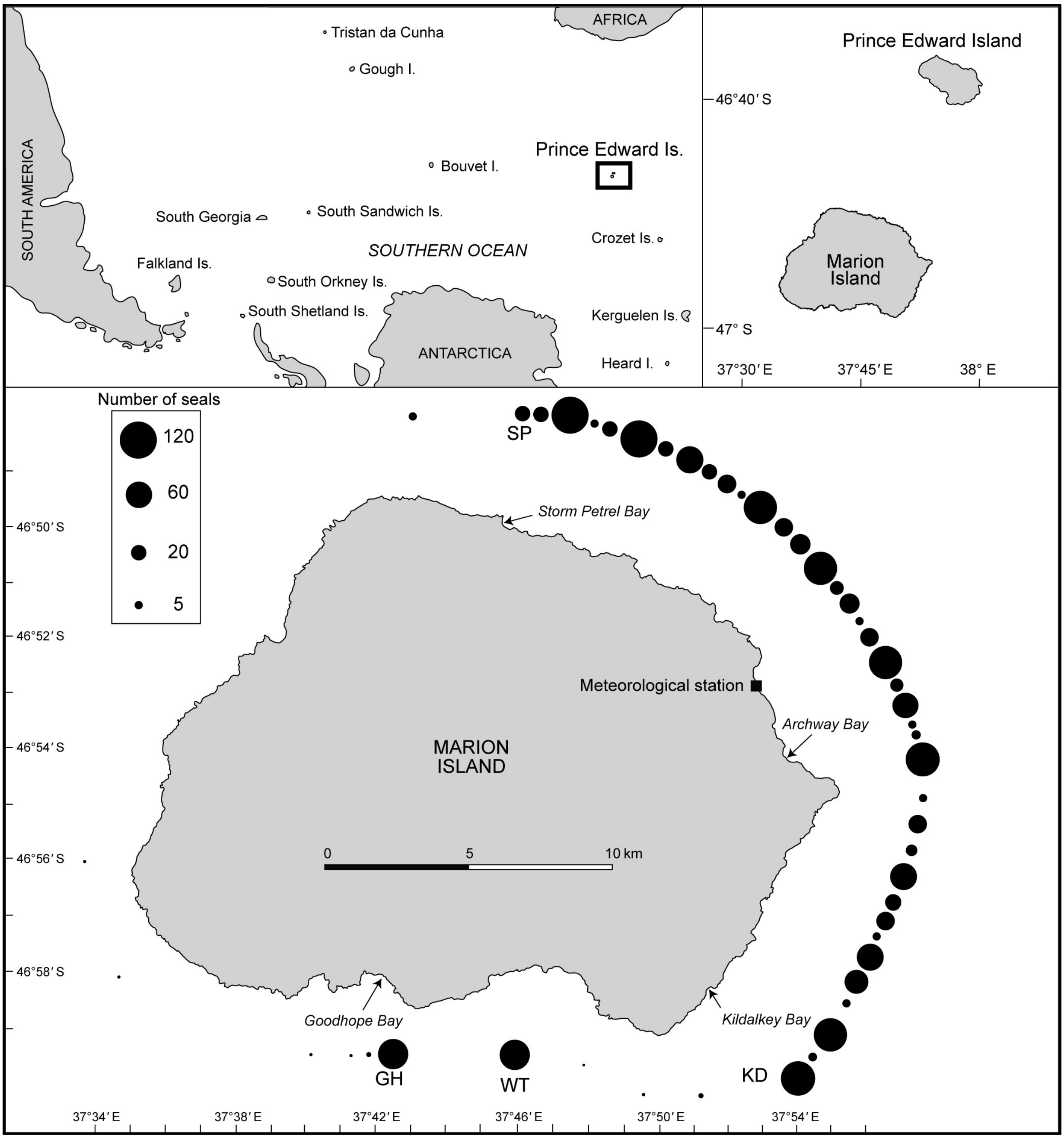

Figure 3.1 Map of Marion Island showing the distribution of southern elephant seals *Mirounga leonina*. The areas of the circles are directly proportional to the mean annual number of elephant seals hauling out at each site. The north and east sections of the coastline between locations marked SP and KD and at locations marked WT and GH form the study area. Reproduced from *African Journal of Marine Science* (2012) 34(3): 373-382 with permission © NISC (Pty) Ltd.

interdigital webbing of each hind flipper of each seal. The colour of the tags was specific to a cohort and the number, to an individual within each cohort, rendering each seal identifiable. Also from 1983 tags were resighted following the pattern detailed in Table 3.1. Resight events, or censuses, of the ESA were conducted approximately four time a month between mid August and the end of September (during the breeding season) and three times per month for the rest of the year. The difference between these periods was to allow for an increase in search effort during that period of the year when elephant seal behaviour made the resighting of tags more difficult. The frequency of haulout meant that most seals were recorded more than once during a particular haulout event. During each census, systematic searches of the ESA for tagged seals were conducted by one or two observers who visited each possible elephant seal haulout sequentially and systematically searched on foot for elephant seals. During censuses the following information was recorded for each tagged seal: colour and number of tag,

Table 3.1 The pattern of resight effort for tagged southern elephant seals *Mirounga leonina* in the Extended Study Area at Marion Island.

Month & Year (inclusive)	Sites and frequency of visits by observers	
	North-East & East Coast (sites MM051 – MM020)	South Coast (Sites MM025 & MM 026)
Nov 1983 – May 1989	Every seven or ten days from Sep – May	Monthly from Sep – May
Aug 1989 – Aug 1992	Every seven or ten days throughout the year	Monthly throughout the year
Sep 1992 – Nov 2003	Every seven or ten days throughout the year	Every seven or ten days throughout the year

location, behaviour and moult status. Where possible, the sex of the seal was also recorded to confirm the determination at tagging.

Data editing

The 35 189 records of male elephant seals collected during the study were edited using the methods detailed in Chapter 2: (1) obviously incorrect or incomplete records were corrected or removed from the database (resultant database of 31 620 records), (2) a single record was chosen to represent each haulout event (15 146 records), and (3) animals older than eight years were removed due to the small sample sizes of older animals participating in haulouts (14 984 records), (4) animals were aged by one year on the 15th of October, unless they had been recorded ashore during a breeding haulout, in which case they had been aged from the beginning of that haulout. To this database were added the calculated distances among all possible haulouts for each individual seal. These distances were determined as the shortest coastline measurements between the centres of each site, ignoring indentations. For each male seal the following 20 haulout events were possible: natal period (N), winter haulouts from age zero to age four (W0 – W4), moult haulouts to age eight (M1 – M8), breeding haulouts from age six to age eight (B6 – B8), the previous breeding (PrB) and previous moult haulouts (PrM) and the haulouts of the first reproductive event (RH1). None of the males was recorded ashore during all of these possible haulout events.

Statistical Approach

The statistical approach followed the methods used in Chapter 2. The structure of the data for comparing two distances D_1 and D_2 (e.g. "*Distance from current haulout to* *natal site*” and “*Distance from current haulout to first winter site*”, respectively) was schematically represented thus:

$$\begin{array}{cc} & \begin{array}{cc} D_1 & D_2 \end{array} \\ \mathbf{X} = & \begin{bmatrix} \mathbf{X_{11}} & \mathbf{0_{12}} \\ \mathbf{0_{21}} & \mathbf{X_{22}} \\ \mathbf{X_{31}} & \mathbf{X_{32}} \end{bmatrix} \end{array}$$

where $\mathbf{X}_{ij} : (n_{ij} \times 1)$ is a column vector of distances for n_{ij} individuals and $\mathbf{O}_{ij} : (n_{ij} \times 1)$ empty data vectors with no observations, with $(i = 1,2,3; \quad j = 1,2)$. $[\text{Note: } n_{31} = n_{32}]$.

We considered different tests for comparing D_1 to D_2 e.g. a mixture of t-tests (paired and two-sample) or a mixture of nonparametric tests (e.g. Wilcoxon Signed Rank and Wilcoxon Rank Sum tests), because the data consists of both paired $(\mathbf{X}_{31}$ and $\mathbf{X}_{32})$ and independent $(\mathbf{X}_{11}$ and $\mathbf{X}_{22})$ data sets. However, because of difficulties in weighting of the components of these mixtures and complications in estimating the standard error, we decided to use the Jackknife approximation (Efron & Tibshirani 1998). This was done because the Jackknife can be considered as a near non parametric test with the characteristic that it is an unbiased estimator of the arithmetic mean, and because the Jackknife, as proposed here, includes all available observations for a specific subset of the data e.g. Case III below.

The test statistic constructed for the general case is $T = a_{11}\overline{\mathbf{X}}_{11} + a_{22}\overline{\mathbf{X}}_{22} + a_{31}\overline{\mathbf{X}}_{31} + a_{32}\overline{\mathbf{X}}_{32}$, where $\overline{\mathbf{X}}_{ij}$ equals the arithmetic mean of the n_{ij} observations from $\mathbf{X}_{ij}$. The weights a_{ij} forms a contrast such that $a_{11} + a_{22} + a_{31} + a_{32} = 0$. Due to incomplete data from a survey and that it was not gained by an experimental design, we identified the following cases (I to V) by which two distances D_1 and D_2 could be compared, namely:

Case I: $n_{11}, n_{22}, n_{31}, n_{32} > 0$, with $a_{11} = -a_{22} = a_{31} = -a_{32} = 1$

Case II: $n_{11}, n_{22} > 0, n_{31} = n_{32} = 0$, with $a_{11} = -a_{22} = 1, \quad a_{31} = a_{32} = 0$

Case III: $n_{11}, n_{31} = n_{32} > 0, n_{22} = 0$, with $2a_{11} = 2a_{31} = -a_{32} = 1, \quad a_{22} = 0$

Case IV: $n_{22}, n_{31} = n_{32} > 0, n_{11} = 0$, with $-2a_{22} = a_{31} = -2a_{32} = 1, \quad a_{11} = 0$

Case V: $n_{31} = n_{32} > 0, \quad n_{11} = n_{22} = 0$, with $a_{31} = -a_{32} = 1, \quad a_{11} = a_{22} = 0$

Depending on the data structure (Cases I to V), Jackknife estimates

$$T_{JK(i)} = \left(a_{11}\mathbf{X}_{11} + a_{22}\mathbf{X}_{22} + a_{31}\mathbf{X}_{31} + a_{32}\mathbf{X}_{32}\right)_{(i)}, i = 1, \ldots, n$$

were obtained with the Jackknife estimator of

T given by $\bar{T}_{JK} = \frac{1}{n}\sum_{i=1}^{n} T_{JK(i)}$ and $SE_{JK} = \left\{\frac{n-1}{n}\sum_{i=1}^{n}\left(T_{JK(i)} - \bar{T}_{JK}\right)^2\right\}^{\frac{1}{2}}$

where $T_{JK(i)}$ is the estimator based on the complete dataset with observation i left out.

To construct CIs (confidence intervals) and hypothesis testing e.g. $\mu_{D_1} = \mu_{D_2}$ the assumption was made that $t_{JK} = \bar{T}_{JK} / SE_{JK}$ can be approximated by a t distribution with $(n-1)$ degrees of freedom.

For the data in question, we selected a subset and applied the procedure applied. All differences were considered statistically significant on a 5% level of significance. Descriptive statistics of the raw data were provided to illustrate the results of the Jackknife. All analyses were completed using SAS (SAS Institute Inc 2004)

Results

Moult haulout

Male elephant seals experiencing their first moult haulout, as yearlings, do not haul out significantly closer to either of the two sites (natal and first winter) that they have previously experienced (Figure 3.2a). At the age of two, males haul out significantly closer to their natal site and their prior winter haulout site than any other sites visited (Figure 3.2b). From the age of three to five years of age, males haul out significantly closer to their previous moult and winter sites than to any sites visited while a young immature animal, but no closer to their previous moult or winter sites than to their natal site or recently visited moult and winter sites (Figures 3.2c – 3.2e). When moulting at age six, male elephant seals haul out closest to their previous moult site, and significantly closer to this site than to their natal site, or sites visited before the age of two Figure 3.2f). Adult males of age seven and eight years, haul out closest to their moult and breeding sites of the previous year, but not significantly closer to these sites than to sites visited recently. They haul out significantly closer to sites of the previous year than to sites visited as a young immature and their natal site (Figures 3.2g – 3.2h).

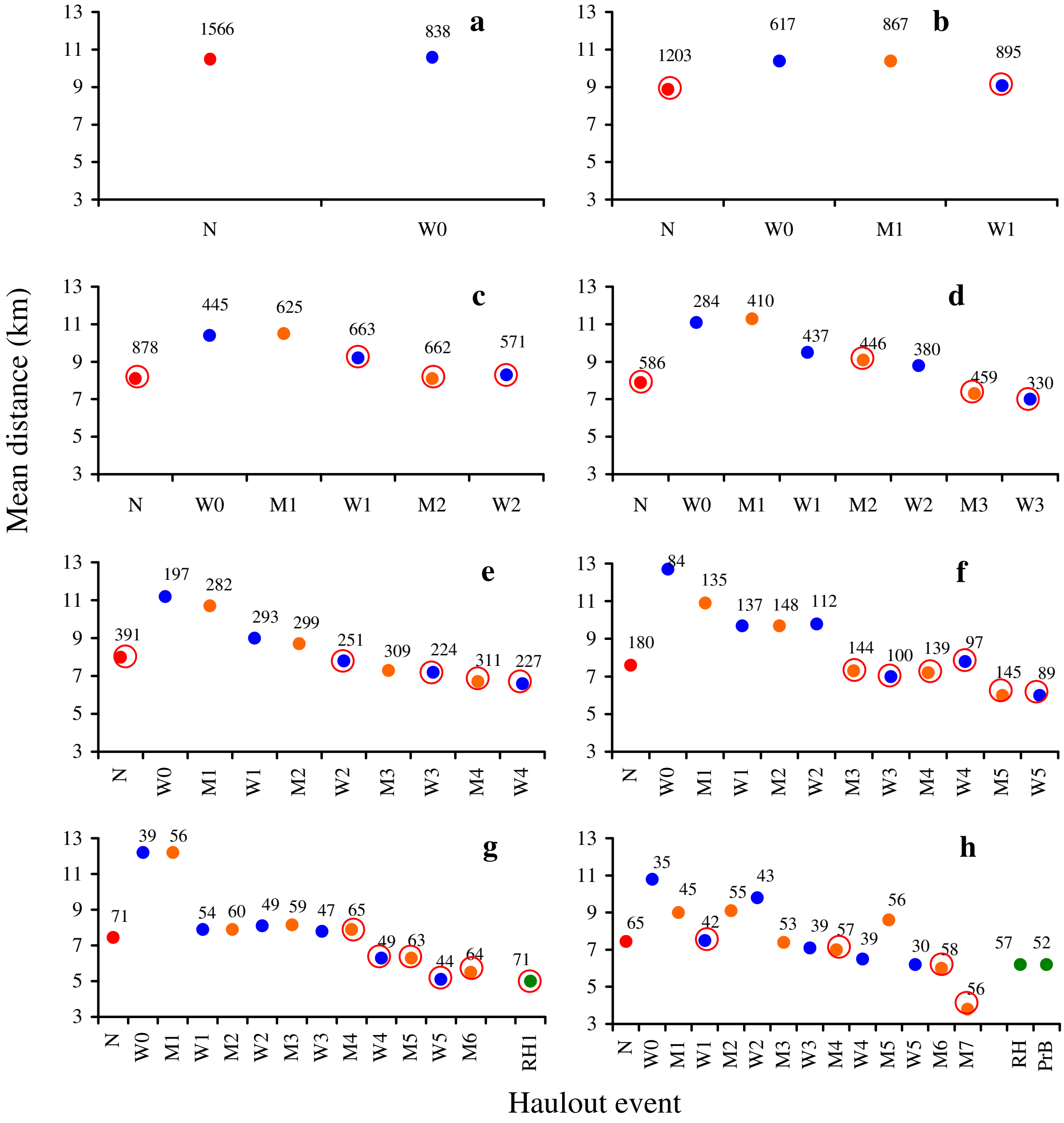

Figure 3.2 Mean distances between the moult sites and various prior haulout sites of male southern elephant seals *Mirounga leonina* of various ages, at Marion Island. Haulout sites are represented by: N – natal site, W0, W1, etc – winter haulout site visited as underyearlings, yearlings, etc respectively; M1, M2, etc – moult sites visited as yearlings, two-year-olds, etc respectively and RH1, PrB – first breeding haulout site and previous breeding haulout site respectively. The numbers above the data points are sample sizes. Elephant seals have hauled out significantly closest to sites represented by circled data points.

Winter haulout

Yearling male southern elephant seals come ashore for their winter haulout significantly closer to their natal site than to any previous haulout site (Figure 3.3a). While older males also haul out close to their natal site, they do not haul out significantly closer to this site than to moult and winter sites used in the last year (Figures 3.3b and 3.3c) or in the last three years (Figure 3.3d). They haul out significantly closer to their previous moult and winter sites than to less recently visited sites.

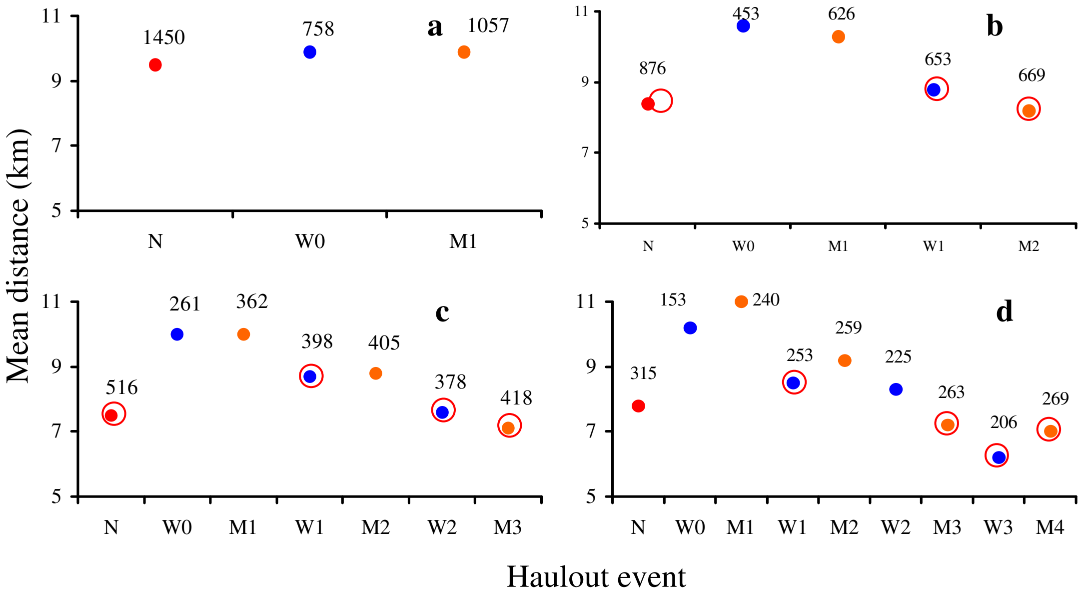

Figure 3.3 Mean distances between the winter haulout sites and various prior haulout sites for male southern elephant seals *Mirounga leonina* of various ages at Marion Island. Haulout sites are represented by: N – natal site, W0, W1, etc – winter haulout site visited as underyearlings, yearlings, etc respectively; M1, M2, etc – moult sites visited as yearlings, two-year-olds etc respectively. The numbers above the data points are sample sizes. Elephant seals have hauled out significantly closest to sites represented by circled data points.

Breeding haulout

Male southern elephant seals breeding for the first time haul out significantly closer to their previous moult site than to most haulout sites visited as an immature. They do not haul out closer to their previous moult site, however, than to their natal site and to most moult sites visited as an immature animal (Figure 3.4a). When hauling out to breed for the second time males haul out no closer to their first breeding site than to their previous two moult sites and their previous winter haulout site. They do haulout significantly closer to their first breeding site than to their natal site and all sites visited as an immature animal (Figure 3.4b). When returning to breed on occasions subsequent to the

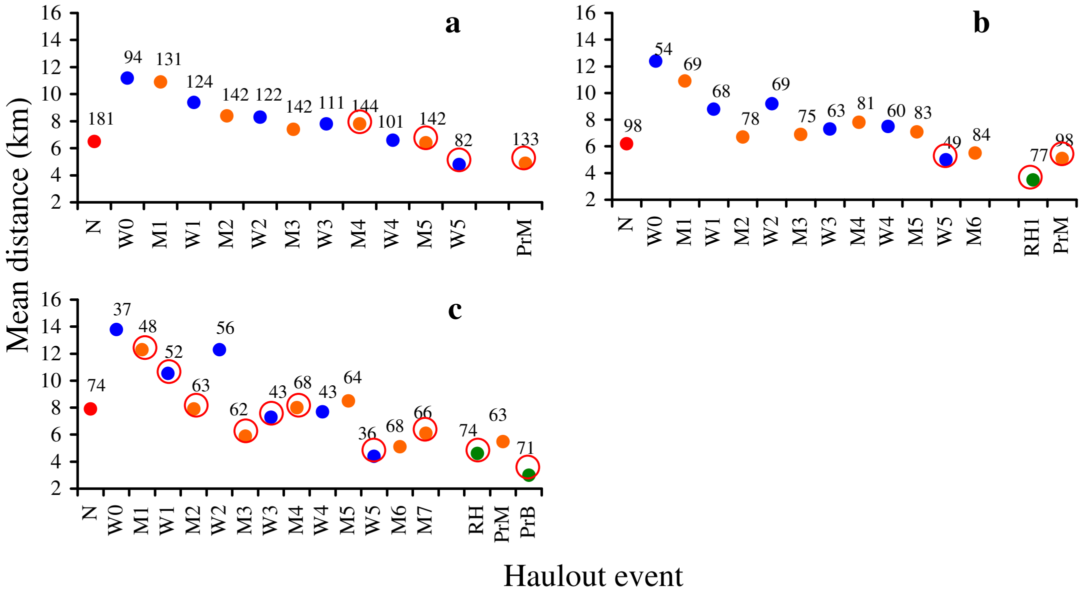

Figure 3.4 Mean distances between the sites of the reproductive haulout events and various prior haulout sites of male southern elephant seals *Mirounga leonina* at Marion Island. Haulout sites are represented by: N – natal site, W0, W1, etc – winter haulout site visited as underyearlings, yearlings, etc respectively; M1, M2, etc – moult sites visited as yearlings, two-year-olds, etc respectively; RH1 – first reproductive haulout site; PrM, PrB – moult site and breeding haulout site of the previous year respectively. The numbers next to each datum point are sample sizes. Elephant seals have hauled out significantly closest to sites represented by the circled data points.

first two, males haul out significantly closer to their previous breeding site except for the winter site visited as a five-year-old (Figure 3.4c).

Table 3.2 Summary of effect of history of movement on choice of haulout site by male southern elephant seals *Mirounga leonina* at Marion Island. N – natal site, Im – moult and winter sites visited when immature, PrIm – haulout site visited as an immature animal on the previous haulout, M – sites visited when moulting, PrM – moult haulout site of the previous year, AdM - moult sites visited as an adult, RH1 – first breeding haulout site, PrB – breeding haulout site of the previous year.

	Current Haulout Event	Previous haulout sites close to the current haulout site	Previous haulout sites distant from the current haulout site
MOULTING	M1	N, Im	
	M2	N, Pr	other Im
	M3	N, recent Im	early Im
	M4	N, recent Im	early Im
	M5	N, recent Im	early Im
	M6 (have not bred)	recent Im	N, early Im
	M7 (have bred)	recent Im, PrM, RH1	N, early Im
	M8 (have bred)	Some Im, PrM	N, most Im, RH1, PrB
WINTER	W1	N, Im	
	W2	N, recent Im	N, other Im
	W3	N, recent Im	N, other Im
	W4	recent Im	N, other Im
BREEDING	RH1	recent Im, PrM	N, early Im
	RH2	PrM, RH1	N, Im
	RH>2	recent Im, RH1, PrB	N, Im, PrM

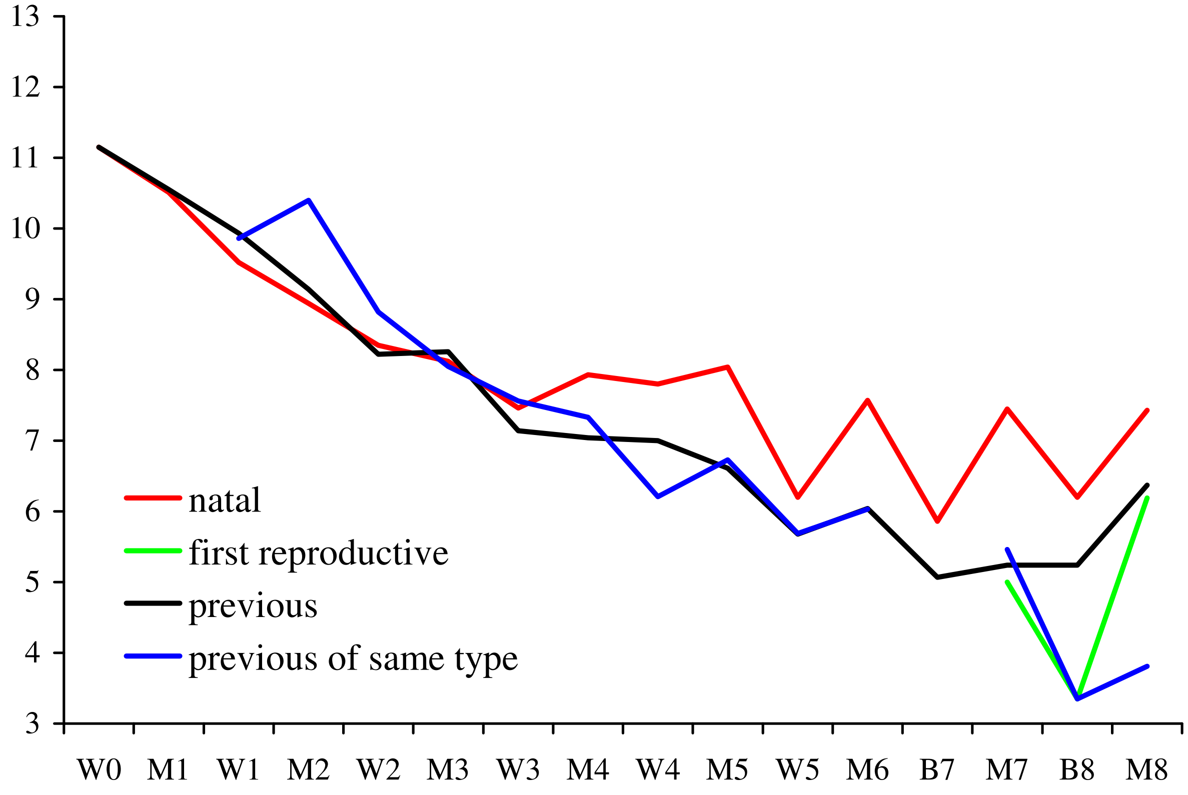

Figure 3.5 Mean distances between current haulout site and selected previous haulout sites by male southern elephant seals *Mirounga leonina* at Marion Island. Current haulout sites are represented by: N – natal site; W0, W1, W2 – winter haulout site visited as underyearlings, yearlings and two-year-olds respectively; M1, M2, etc – moult sites visited as yearlings, two-year-olds, etc respectively; B4, B5, etc – breeding sites visited as four-year-olds, five-year-olds, etc, respectively.

Discussion

In this study we attempted to define the pattern of site fidelity followed by male southern elephant seals over the course of their lives. Specifically we asked whether male elephant seals showed fidelity to any sites other than their natal and first breeding site, whether fidelity was linked to the purpose of the current haulout, and whether this changed over the course of their lives. Furthermore, we asked whether this differed from the pattern shown by females.

Site fidelity of males

As immature animals, whether hauling out during the winter or to moult, male seals hauled out significantly closest to their natal site and recently visited sites and distant from sites visited as young immature animals (Figure 3.5 and Table 3.2). When returning to moult as adults, however, they hauled out closer to recently visited sites than to their natal site or sites visited as young immature animals. When they first hauled out to breed, male seals hauled out closer to recently visited sites, including their previous moult site, than to their natal site or sites visited early in immaturity. Returning to breed a second time, they hauled out closest to their first breeding site and their previous moult site, and distant from sites visited as immature animals. Animals returning to breed subsequently, hauled out closest to previous breeding and moult site, and some sites visited as an immature animal, and distant only from their natal site and a number of sites visited as an immature.

As with female elephant seals at the study site (see Chapter 2), the data reported here add considerably to the described patterns of dispersal by elephant seals and other pinnipeds. Elephant seals from a number of populations show fidelity to a previous site (Carrick & Ingham 1962a, b; Nichols 1970; Bester & van Niekerk 1984; Campagna & Lewis 1992; Galimberti & Boitani 1999; Van den Hoff 2001) and a number of studies have indicated that females show fidelity to their natal site and first breeding site (Carrick & Ingham 1962b; Nichols 1970; Hindell & Little 1988; Huber *et al.* 1991). However, due to their greater age than females at the onset of breeding (Laws 1993) and lower survival than females (Pistorius et al 1999), few studies have been able to assess the natal site fidelity of large groups of male elephant seals. Studies of dispersal in males have mostly considered site fidelity in animals marked as adults (Carrick & Ingham 1962a; Nichols 1970; Campagna & Lewis 1992). While these indicate that male southern elephant seals show fidelity to a previous haulout site, the lack of information as to the age of the animal when tagged, and the location of the natal site, undermines the value of these observations and does not allow true comparisons among sexes or age groups. Hofmeyr (2000) examined site fidelity of elephant seals from the study population that had only marked at their natal site as pups. While significant fidelity by both sexes and various age classes was found to their natal site and site of first reproductive event, and significant difference were found between the patterns of dispersal of the two sexes, site fidelity in relation to other haulout sites was not considered. By examining fidelity over the course of their lives, this study gives a more complete picture of the haulout behaviour of male elephant seals and the possible choices that they make in selecting a site.

Differences between the sexes

Many species of pinnipeds show considerable differences between the sexes in terms of morphology (Bininda-Emonds & Gittleman 2000; Lindenfors *et al.* 2002), foraging behaviour and diet (Castley *et al.* 1991; Beck *et al.* 2005; Page *et al.* 2005; Breed *et al.* 2006; Page *et al.* 2006; Beck *et al.* 2007a; Beck *et al.* 2007b; Meynier *et al.* 2008; Staniland & Robinson 2008; Trites & Calkins 2008; Hofmeyr *et al.* 2010), habitat use (Page *et al.* 2006; Staniland & Robinson 2008) and life history (Payne 1977; Lander 1981; Warneke & Shaughnessy 1985; Trillmich 1987; Laws 1993; Butterworth *et al.* 1995). Elephant seals are an extreme example in this regard, with males weighing up to ten times the mass of females (Laws 1993). Males and females differ in their diet, foraging areas used and dive characteristics (Hindell 1991; McConnell *et al.* 1992; Campagna *et al.* 1995; Campagna *et al.* 1999; Lewis *et al.* 2006; Campagna *et al.* 2007; Field *et al.* 2007; Biuw *et al.* 2010; McIntyre *et al.* 2010a; McIntyre *et al.* 2010b). Furthermore, the timing of their haulout events, particularly during the breeding season is very different (Laws 1956; Carrick & Ingham 1962a; Condy 1979; Kirkman *et al.* 2003; Kirkman *et al.* 2004; McIntyre *et al.* 2010a). While individual females will spend a single month ashore during the breeding season, individual males will remain ashore for a more variable period, and up to three months. And lastly, Mulaudzi *et al.* (2008) demonstrated that male and female southern elephant seals preferred, and discriminated against, overlapping but different suites of haulout sites, which varied according to the haulout type. Furthermore, they showed that differences between the sexes in site selection became more apparent with age.

Given the differences between males and females in all of these aspects, substantial differences in patterns of site selection and site fidelity are expected, and indeed, are found. While females show significantly greater fidelity to their natal site than to other sites only when they are yearlings and when they first haul out to breed (see Chapter 2), males showed preferential fidelity to this site throughout their subadult years, but not as an adult, including their first breeding haulout. However, both males and females tend to show greater fidelity to recent haulouts throughout their lives. For females these haulouts are usually of the same type as the current haulout, whereas for males, these are both breeding and moult haulouts.

Although males show greater fidelity to recently visited sites than to their natal site when they first haul out to breed, and females show significantly greater fidelity to their natal site than to all other sites visited at their first recorded breeding event, males do breed significantly closer to their natal site than females during this event. The latter was explained by Hofmeyr (2000) as possibly due to the differences in the life histories of the sexes; females give birth within days of their arrival during the breeding season (Carrick *et al.* 1962b; Ling & Bryden 1992; Wilkinson 1992) and are unable to move among sites thereafter since their pup is both dependent and relatively immobile (Condy 1979; Wilkinson 1992), whereas males are able to move among sites throughout the breeding season. Munyai (2006) showed that this was the case, with males moving significantly farther than females, and three times as often, during a breeding haulout. Assessing fidelity to other sites in addition to the natal site, gives a more complete picture of site selection by male elephant seals. Although most haul out in the vicinity of their natal site (60 % within five kilometres at the first breeding haulout, and 88 % on subsequent breeding haulouts – Hofmeyr 2000), it is possible that they have some degree of familiarity with the various sites in this area by virtue of their spatial memory of previous visits. Their decision concerning the site to be selected may be based on this familiarity. The role that spatial memory plays in selecting a site may be mediated to some degree by social information. A number of species of animals have been shown to select sites based on the presence or numbers of conspecifics at a site (Danchin & Wagner 1997; Courchamp *et al.* 1999; Valone 2007). In addition, many species also show evidence of being able to assess opponent fighting ability (Freeman 1987; Johnson & Ackerman 1998; Oliveira *et al.* 1998; Earley & Dugatkin 2002; Earley *et al.* 2005) which may play a role in habitat selection. Male elephant seals may therefore partially select a site based on the quantity of adult females and the quality of adult males present.

The process of breeding habitat selection by females is possibly far simpler than that of males. As noted, due to parturition taking place shortly after arrival at a terrestrial haulout (Carrick *et al.* 1962b; Ling & Bryden 1992; Wilkinson 1992), their ability to select an alternative landfall is compromised. They should therefore navigate more carefully than males to their first landfall during the breeding haulout. Whether they do so is unknown. To answer this question, data on the site selection of elephant seals would have to be collected at a finer temporal resolution than in the current study. Females may, as is suggested for males, modify their choice of a breeding site based on social information. The presence of other females may determine whether they stay at their first landfall or move on. Anderson *et al.* (1975) suggested that the breeding locations of female grey seals *Halichoerus grypus* is determined by those that arrive early in the season, since they are gregarious animals. They also suggested, however, that female grey seals moved several times before selecting a pupping site.

An important question is why females do not navigate with greater accuracy to a previous site than recorded. Female otariids are able to do so, pupping within metres of previous pupping sites, despite giving birth shortly after arrival (Lunn & Boyd 1991; Baker *et al.* 1995). Female grey seals also frequently give birth within metres of a previous pupping site (Boness & James 1979; Pomeroy *et al.* 1994). It is quite possible, however, that in a low density elephant seal population like that at Marion Island, with a number of relatively small and similarly size harems on suitable beaches (Wilkinson 1992), the differences in reproductive success accruing to females from choice of a specific site, are not significant. Since they only give birth to a single pup, any one of a number of beaches at which female elephant seals can raise their pup to weaning, should be suitable (Laws 1993). Males, on the other hand, are potentially able to father many offspring in a single season (McCann 1981; Le Boeuf & Reiter 1988; Fabiani *et al.* 2004). Selecting a site based on prior local spatial familiarity and current social knowledge, may make a great difference to their reproductive success.

References

ANDERSON, S.S., BURTON, R.W. & SUMMERS, C.F. 1975. Behaviour of grey seals (*Halichoerus grypus*) during a breeding season at North Rona. *Journal of Zoology, London* **177:** 179-195.

BAKER, J.D., ANTONELIS, G.A., FOWLER, C.W. & YORK, A.E. 1995. Natal site fidelity in northern fur seals, *Callorhinus ursinus*. *Animal Behaviour* **50:** 237-247.

BECK, C.A., IVERSON, S.J. & BOWEN, W.D. 2005. Blubber fatty acids of gray seals reveal sex differences in the diet of a size-dimorphic marine carnivore. *Canadian Journal of Zoology* **83:** 377-388.

BECK, C.A., IVERSON, S.J., BOWEN, W.D. & BLANCHARD, W. 2007a. Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative fatty acid signature analysis. *Journal of Animal Ecology* **76:** 490-502.

BECK, C.A., REA, L.D., IVERSON, S.J., KENNISH, J.M., PITCHER, K.W. & FADELY, B.S. 2007b. Blubber fatty acid profiles reveal regional, seasonal, age-class and sex differences in the diet of young Steller sea lions in Alaska. *Marine Ecology Progress Series* **338:** 269-280.

BESTER, M.N. & PANSEGROUW, H.M. 1992. Ranging behaviour of southern elephant seal cows from Marion Island. *South African Journal of Science* **88:** 574-577.

BESTER, M.N. & VAN NIEKERK, J.L. 1984. *Dispersie van suidelike olifantrobbe Mirounga leonina te die Courbet Skiereiland, Iles Kerguelen*. Internal report, Mammal Research Institute, University of Pretoria, Pretoria. 41 pp.

BININDA-EMONDS, O.R.P. & GITTLEMAN, J.L. 2000. Are pinnipeds functionally different from fissiped carnivores? The importance of phylogenetic comparative analyses. *Evolution* **54:** 1011-1023.

BIUW, M., NØST, O.A., STIEN, A., ZHOU, Q., LYDERSEN, C. & KOVACS, K.M. 2010. Effects of Hydrographic Variability on the Spatial, Seasonal and Diel Diving Patterns of Southern Elephant Seals in the Eastern Weddell Sea. *PLoS ONE* **5:** e13816.

BONESS, D.J. & JAMES, H. 1979. Reproductive behaviour of the grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. *Journal of Zoology, London* **188:** 477-500.

BREED, G.A., BOWEN, W.D., MCMILLAN, J.I. & LEONARD, M.L. 2006. Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. *Proceedings of the Royal Society of London B* **273:** 2319-2326.

BUTTERWORTH, D.S., PUNT, A.E., OOSTHUIZEN, W.H. & WICKENS, P.A. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 3. Modelling the dynamics of the Cape fur seal *Arctocephalus pusillus pusillus*. *South African Journal of Marine Science* **16:** 161-183.

CAMPAGNA, C., FEDAK, M.A. & MCCONNELL, B.J. 1999. Post-breeding distribution and diving behavior of adult male southern elephant seals from Patagonia. *Journal of Mammalogy* **80:** 1341-1352.

CAMPAGNA, C., LE BOEUF, B.J., BLACKWELL, S.B., CROCKER, D.E. & QUINTANA, F. 1995. Diving behaviour and foraging location of female southern elephant seals from Patagonia. *Journal of Zoology, London* **236:** 55-71.

CAMPAGNA, C. & LEWIS, M. 1992. Growth and distribution of a southern elephant seal colony. *Marine Mammal Science* **8:** 387-396.

CAMPAGNA, C., PIOLA, A.R., ROSA-MARIN, M., LEWIS, M., ZAJACZKOVSKI, U. & FERNÁNDEZ, T. 2007. Deep divers in shallow seas: southern elephant seals on the Patagonian shelf. *Deep Sea Research I* **54:** 1792-1814.

CANTOS, F.J. & TELLERIA, J.L. 1994. Stopover site fidelity of four migrant warblers in the Iberian Peninsula. *Journal of Avian Biology* **25:** 131-134.

CARRICK, R., CSORDAS, S.E., INGHAM, S.E. & KEITH, K. 1962a. Studies of the southern elephant seal, *Mirounga leonina* (L.). III. The annual cycle in relation to age and sex. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 119-160.

CARRICK, R., CSORDAS, S.E., INGHAM, S.E. & KEITH, K. 1962b. Studies on the southern elephant seal, *Mirounga leonina* (L.). III. The annual cycle in relation to age and sex. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 119-160.

CARRICK, R. & INGHAM, S.E. 1962a. Studies on the southern elephant seal, *Mirounga leonina* (L.) I. Introduction to the series. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 89-101.

CARRICK, R. & INGHAM, S.E. 1962b. Studies on the southern elephant seal, *Mirounga leonina* (L.) V. Population dynamics and utilization. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 198-206.

CASTLEY, J.G., COCKCROFT, V.G. & KERLEY, G.I.H. 1991. A note on the stomach contents of fur seals *Arctocephalus pusillus pusillus* beached on the south-east coast of South Africa. *South African Journal of marine Science* **11:** 573-577.

CLOBERT, J., DANCHIN, E., DHONDT, A. & NICHOLS, J.D. 2001. *Dispersal.* Oxford University Press, Oxford. 452 pp.

CONDY, P.R. 1979. Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.) at Marion Island. *South African Journal of Zoology* **14:** 95-102.

COURCHAMP, F., CLUTTON-BROCK, T. & GRENFELL, B. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution* **14:** 405-410.

DANCHIN, E. & WAGNER, R.H. 1997. The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology and Evolution* **12:** 342-347.

DE BRUYN, P.J.N. 2009. Life history studies of the southern elephant seal population at Marion Island. Ph.D., University of Pretoria, Pretoria.

DOBSON, F.S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour* **30:** 1183-1192.

EARLEY, R.L., DRUEN, M. & DUGATKIN, L.A. 2005. Watching fights does not alter a bystander's response towards naïve conspecifics in male green swordtail fish, *Xiphophorus helleri*. *Animal Behaviour* **69:** 1139-1145.

EARLEY, R.L. & DUGATKIN, L.A. 2002. Eavesdropping on visual cues in green swordtail (Xiphophorus helleri) fights: a case for networking. *Proceedings of the Royal Society of London B* **269:** 943-952.

EFRON, B. & TIBSHIRANI, R.J. 1998. *An introduction to the bootstrap.* Chapman and Hall / CRC Press, New York. 456 pp.

FABIANI, A., GALIMBERTI, F., SANVITO, S. & HOELZEL, A.R. 2004. Extreme polygyny among southern elephant seals on Sea Lion Island, Falkland Islands. *Behavioral Ecology* **15:** 961-969.

FEDAK, M.A., ARNBOM, T.A., MCCONNELL, B.J., CHAMBERS, C., BOYD, I.L., HARWOOD, J. & MCCANN, T.S. 1994. Expenditure, investment, and acquisition of energy in southern elephant seals. In: *Elephant seals: population ecology, behaviour and physiology*, (ed) B.J. Le Boeuf & R.M. Laws, pp. 354-373. University of California Press, Berkeley.

FIELD, I.C., BRADSHAW, C.J.A., BURTON, H.R. & HINDELL, M.A. 2007. Differential resource allocation strategies in juvenile elephant seals in the highly seasonal Southern Ocean. *Marine Ecology Progress Series* **331:** 281-290.

FOOTE, A.D., SIMILÄ, T., VÍKINGSSON, G.A. & STEVICK, P.T. 2010. Movement, site fidelity and connectivity in a top marine predator, the killer whale. *Evolution and Ecology* **24:** 803-814.

FREEMAN, S. 1987. Male red-winged blackbirds (*Agelaius phoeniceus*) assess the RHP of neighbors by watching contests. *Behavioral Ecology and Sociobiology* **21:** 307-311.

GALIMBERTI, F. & BOITANI, L. 1999. Demography and breeding biology of a small, localized population of southern elephant seals (*Mirounga leonina*). *Marine Mammal Science* **15:** 159-178.

GREENWOOD, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* **28:** 1140-1162.

HAMER, K.C., PHILLIPS, R.A., HILL, J.K., WANLESS, S. & WOOD, A.G. 2001. Contrasting foraging strategies of gannets *Morus bassanus* at two North Atlantic colonies: foraging trip duration and foraging area fidelity. *Marine Ecology Progress Series* **224:** 283-290.

HESTBECK, J.B., NICHOLS, J.D. & MALECKI, R.A. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecology* **72:** 523-533.

HINDELL, M.A. 1991. Some lif-history parameters of a declining population of southern elephant seals, *Mirounga leonina*. *Journal of Animal Ecology* **60:** 119-134.

HINDELL, M.A. & BURTON, H.R. 1988. The history of the elephant seal industry at Macquarie Island and an estimate of the pre-sealing numbers. *Papers and Proceedings of the Royal Society of Tasmania* **122:** 159-168.

HINDELL, M.A. & LITTLE, G.J. 1988. Longevity, fertility and philopatry of two female southern elephant seals (*Mirounga leonina*) at Macquarie Island. *Marine Mammal Science* **4:** 168-171.

HOFMEYR, G.J.G. 2000. Dispersal and dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. M.Sc., University of Pretoria, Pretoria.

HOFMEYR, G.J.G., BESTER, M.N., KIRKMAN, S.P., LYDERSEN, C. & KOVACS, K.M. 2010. Intraspecific differences in the diet of Antarctic fur seals at Nyrøysa, Bouvetøya. *Polar Biology* **33:** 1171-1178.

HUBER, H.R., ROVETTA, A.C., FRY, L.A. & JOHNSTON, S. 1991. Age-specific natality of northern elephant seals at the South Farallon Islands, California. *Journal of Mammalogy* **72:** 525-534.

JOHNSON, J.I. & ACKERMAN, A. 1998. Watch and learn: preview of the fighting ability of opponents alters contest behaviour strategy. *Animal Behaviour* **56:** 771-776.

JONKER, F.C. & BESTER, M.N. 1998. Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island. *Antarctic Science* **10:** 21-30.

KIRKMAN, S.P., BESTER, M.N., HOFMEYR, G.J.G., JONKER, F.C., PISTORIUS, P.A., OWEN, R. & STRYDOM, N. 2004. Variation in the timing of the breeding haulout of female southern elephant seals at Marion Island. *Australian Journal of Zoology* **52:** 379-388.

KIRKMAN, S.P., BESTER, M.N., PISTORIUS, P.A., HOFMEYR, G.J.G., JONKER, F.C., OWEN, R. & STRYDOM, N. 2003. Variation in the timing of moult of southern elephant seals at Marion Island *South African Journal of Wildlife Research* **33:** 79-84.

KIRKMAN, S.P., BESTER, M.N., PISTORIUS, P.A., HOFMEYR, G.J.G., OWEN, R. & MECENERO, S. 2001. Participation in the winter haulout by southern elephant seals (*Mirounga leonina*). *Antarctic Science* **13:** 380-384.

LANDER, R.H. 1981. A life table and biomass estimate for Alaskan fur seals. *Fisheries Research* **1:** 55-70.

LAWS, R.M. 1956. The elephant seal (*Mirounga leonina* Linn.). II. General social and reproductive behaviour. *Falkland Islands Dependencies Survey Scientific Reports* **13:** 1-88.

LAWS, R.M. 1993. Identification of species. In: *Antarctic seals: research methods and techniques*, (ed) R.M. Laws, pp. 1-28. Cambridge University Press, Cambridge.

LE BOEUF, B.J. & LAWS, R.M. 1994. Elephant seals: an introduction to the genus. In: *Elephant seals: population ecology, behaviour and physiology*, (ed) B.J. Le Boeuf & R.M. Laws, pp. 1-26. University of California Press, Berkeley.

LE BOEUF, B.J. & REITER, J. 1988. Lifetime reproductive success in northern elephant seals. In: *Reproductive success: studies of individual variation in contrasting breeding systems*, (ed) T.H. Clutton-Brock, pp. 344-362. University of Chicago Press, Chicago.

LEWIS, R., O'CONNELL, T.C., LEWIS, M., CAMPAGNA, C. & HOELZEL, A.R. 2006. Sex-specific foraging strategies and resource partitioning in the southern elephant seal (*Mirounga leonina*). *Proceedings of the Royal Society B* **273:** 2901-2907.

LINDENFORS, P., TULLBERG, B.S. & BIUW, M. 2002. Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behavioral Ecology and Sociobiology* **52:** 188-193.

LING, J.K. & BRYDEN, M.M. 1992. *Mirounga leonina*. *Mammalian Species* **391:** 1-8.

LUNN, N.J. & BOYD, I.L. 1991. Pupping site fidelity of Antarctic fur seals at Bird Island, South Georgia. *Journal of Mammalogy* **72:** 202-206.

MCCANN, T.S. 1981. Aggression and sexual activity of male southern elephant seals, *Mirounga leonina*. *Journal of Zoology, London* **195:** 295-310.

MCCONNELL, B.J., CHAMBERS, C. & FEDAK, M.A. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarctic Science* **4:** 393-398.

MCINTYRE, T., DE BRUYN, P.J.N., ANSORGE, I.J., BESTER, M.N., BORNEMANN, H., PLÖTZ, J. & TOSH, C.A. 2010a. A lifetime at depth:

vertical distribution of southern elephant seals in the water column. *Polar Biology* **33:** 1037-1048.

MCINTYRE, T., TOSH, C.A., PLÖTZ, J., BORNEMANN, H. & BESTER, M.N. 2010b. Segregation in a sexually dimorphic mammal: a mixed-effects modelling analysis of diving behaviour in southern elephant seals. *Marine Ecology Progress Series* **412:** 293-304.

METCALFE, N.B. & FURNESS, R.W. 1985. Survival, winter population stability and site fidelity in the Turnstone *Arenaria interpres*. *Bird Study* **32:** 207-214.

MEYNIER, L., MOREL, P.C.H., CHILVERS, B.L., MACKENZIE, D.D.S., MACGIBBON, A. & DUIGNAN, P.J. 2008. Temporal and sex differences in the blubber fatty acid profiles of the New Zealand sea lion *Phocarctos hookeri*. *Marine Ecology Progress Series* **366:** 271-279.

MULAUDZI, T.W., HOFMEYR, G.J.G., BESTER, M.N., KIRKMAN, S.P., PISTORIUS, P.A., JONKER, F.C., MAKHADO, A.B., OWEN, J.H. & GRIMBEEK, R.J. 2008. Haulout site selection by southern elephant seals at Marion Island. *African Zoology* **43:** 25-33.

MUNYAI, F.M. 2006. Intersite movement by southern elephant seals ashore at Marion Island. M.Sc., University of Pretoria, Pretoria.

MURPHY, R.C. 1914. Notes on the sea elephant *Mirounga leonina* (Linné). *Bulletin of the American Museum of Natural History* **33:** 63-86.

NICHOLS, D.G. 1970. Dispersal and dispersion in relation to the birthsite of the southern elephant seal, *Mirounga leonina* (L.), of Macquarie Island *Mammalia* **34:** 598-616.

OLIVEIRA, R.F., MCGREGOR, P.K. & LATRUFFE, C. 1998. Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proceedings of the Royal Society of London, Series B* **265:** 1045-1049.

PAGE, B., MCKENZIE, J. & GOLDSWORTHY, S.D. 2005. Inter-sexual differences in New Zealand fur seal diving behaviour. *Marine Ecology Progress Series* **304:** 249-264.

PAGE, B., MCKENZIE, J., SUMNER, M.D., COYNE, M. & GOLDSWORTHY, S.D. 2006. Spatial separation of foraging habitats among New Zealand fur seals. *Marine Ecology Progress Series* **323:** 263–279.

PAYNE, M.R. 1977. Growth of a fur seal population. *Philosophical Transactions of the Royal Society, London, B* **279:** 67-79.

PISTORIUS, P.A., BESTER, M.N., LEWIS, M.N., TAYLOR, F.E., CAMPAGNA, C. & KIRKMAN, S.P. 2004. Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal (*Mirounga leonina*). *Journal of Zoology, London* **263:** 107-119.

PISTORIUS, P.A., DE BRUYN, P.J.N. & BESTER, M.N. 2011. Population dynamics of southern elephant seals: a synthesis of three decades of demographic research at Marion Island. *South African Journal of marine Science* **33:** 523-534.

PISTORIUS, P.A., KIRKMAN, S.P., BESTER, M.N. & TAYLOR, F.E. 2002. Implications of the winter haulout for future survival and resighting probablity of southern elephant seals at Marion Island. *South African Journal of Wildlife Research* **32:** 59-63.

POMEROY, P.P., ANDERSON, S.S., TWISS, S.D. & MCCONNELL, B.J. 1994. Dispersion and site fidelity of breeding female grey seals (*Halichoerus grypus*) on North Rona, Scotland. *Journal of Zoology, London* **233:** 429-447.

REED, E.T., COOCH, E.G., GOUDIE, R.I. & COOKE, F. 1998. Site fidelity of black brant wintering and spring staging in the Strait of Georgia, British Columbia. *The Condor* **100:** 426-437.

ROBERTSON, G.J. & COOKE, F. 1999. Winter philopatry in migratory waterfowl. *The Auk* **116:** 20-34.

SAS.INSTITUTE.INC. 2004. *SAS/STAT 9.1 users guide.* SAS Institute Inc., Cary, N.C. pp.

SHIELDS, W.M. 1987. Dispersal and mating systems: investigating their causal connections. In: *Mammalian dispersal patterns: the effects of social structure on population genetics*, (ed) B.D. Chepko-Sade & Z.T. Halpin, pp. 3-24. University of Chicago Press, Chicago.

STANILAND, I.J. & ROBINSON, S.L. 2008. Segregation between the sexes: Antarctic fur seals, Arctocephalus gazella, foraging at South Georgia. *Animal Behaviour* **75:** 1581-1590.

TRILLMICH, F. 1987. Galapagos fur seal, *Arctocephalus galapagoensis*. In: *Status, biology and ecology of fur seals. Proceedings of an international symposium and workshop, Cambridge, England, 23–27 April 1984.* , (ed) J.P. Croxall & R.L. Gentry, pp. NOAA Technical report NMFS **51:** 23-28,

TRITES, A.W. & CALKINS, D.G. 2008. Diets of mature male and female Steller sea lions (*Eumetopias jubatus*) differ and cannot be used as proxies for each other. *Aquatic Mammals* **34:** 25-34.

VALONE, T.J. 2007. From eavesdropping on performance to copying the behavior of others: a review of public information use. *Behavioral Ecology and Sociobiology* **62:** 1-14.

VAN DEN HOFF, J. 2001. Dispersal of southern elephant seals (*Mirounga leonina* L.) marked at Macquarie Island. *Wildlife Research* **28:** 413-418.

WARNEKE, R.M. & SHAUGHNESSY, P. 1985. *Arctocephalus pusillus*, the South African and Australian fur seal: Taxonomy, evolution, biogeography, and life history. In: *Studies of sea mammals in south latitudes*, (ed) J.K. Ling & M.M. Bryden, pp. 53-77. South Australia Museum, Adelaide.

WILKINSON, I.S. 1992. Factors affecting reproductive success of southern elephant seals, *Mirounga leonina*, at Marion Island. Ph.D., University of Pretoria, Pretoria.

WILKINSON, I.S. & BESTER, M.N. 1990. Duration of post-weaning fast and local dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. *Journal of Zoology, London* **222:** 591-600.

Chapter 4 ▪ Natal site fidelity by breeding female southern elephant seals in relation to their history of participation in the winter haulout

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Does participation in a winter haulout by female southern elephant seals serve to maintain fidelity to their natal site?

Immature southern elephant seal, Trypot Beach, Marion Island. Photo – G. Hofmeyr

"The adaptive significance of virtual detachment from the sea during breeding and moulting is fairly obvious, but the autumn-winter haul-out presents a puzzle"

Robert Carrick, Stefan Csordas, Susan Ingham & Kent Keith (1962b)

Published as:

Natal Site Fidelity by Breeding Female Southern Elephant seals in Relation to their History of Participation in the Winter Haulout

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CHAPTER 4

NATAL SITE FIDELITY BY BREEDING FEMALE SOUTHERN ELEPHANT SEALS IN RELATION TO THEIR HISTORY OF PARTICIPATION IN THE WINTER HAULOUT

Abstract

Of the four types of terrestrial haulout periods undertaken by southern elephant seals (*Mirounga leonina*), only the purpose of the winter haulout is unknown. Since returning to a haulout site from distant pelagic foraging grounds bears significant costs in terms of increased energy expenditure, reduced foraging time and increased exposure to predation, each haulout must serve a purpose. We examined the hypothesis that the winter haulout serves to maintain familiarity with the natal site, thereby increasing site fidelity. To this end we analysed a long term mark-recapture data set for female southern elephant seals at Marion Island, Southern Ocean. Results indicate that, whereas greater natal site fidelity as primiparous females was associated with recorded presence ashore at the study site during the winter haulout as immatures, this was not the case for multiparous females. Furthermore, recorded presence ashore during both the moult haulouts as immatures, and all haulouts as immatures, irrespective of haulout type, was also associated with increased site fidelity. This suggests that any haulout at the natal island as an immature seal, whether for the moult or winter haulout, assists in maintaining site fidelity. Therefore, while the winter haulout facilitates greater natal site fidelity, whether this is the sole reason for this terrestrial period remains uncertain.

Keywords: animal movement, dispersal, *Mirounga leonina*, Subantarctic

Introduction

Southern elephant seals (*Mirounga leonina*) are the largest of all pinnipeds, with some adult males reaching three tons (Laws 1993). They inhabit the waters of the Southern Ocean, spending some 70-85 % of their lives at sea (Carrick *et al.* 1962a; McIntyre *et al.* 2010). They undertake a highly synchronized bi-annual migration between pelagic foraging grounds and haulout sites on isolated Subantarctic islands (Carrick *et al.* 1962a; Hindell & Burton 1988; Bester & Pansegrouw 1992b; Jonker & Bester 1998). Southern elephant seals are ashore for four types of protracted terrestrial periods during the course of their lives: (1) during the natal period, pups will spend 2-3 months ashore after birth and prior to going to sea for the first time; (2) all southern elephant seals participate in the annual moult haulout of approximately a month (excluding pups of the year, which moult at three weeks of age); (3) the majority of adults will participate in an annual breeding haulout; and (4) the winter haulout (Laws 1956; Carrick *et al.* 1962a; Hindell & Burton 1988; Wilkinson 1992; Le Boeuf & Laws 1994). The winter haulout, also termed the resting haulout, mid-year haulout or autumn-winter haulout (Carrick *et al.* 1962b; Burton 1985; Wilkinson 1992; Wheatley 2001), is undertaken during the austral autumn and winter, predominantly by immature animals (Laws 1956; Carrick *et al.* 1962a; Condy 1979; Hindell & Burton 1988; Kirkman *et al.* 2001).

Returning to a terrestrial haulout site bears significant costs. Elephant seal foraging areas and haulout sites are usually far apart, typically a few hundred or thousand kilometres and seals must therefore expend much time and energy migrating between sites (Hindell & Burton 1988; Bester & Pansegrouw 1992b; Jonker & Bester 1998; Field *et al.* 2001; Biuw *et al.* 2007; Tosh *et al.* 2009; Bailleul *et al.* 2010; McIntyre *et al.* 2011). Further costs are incurred due to the fast that accompanies a terrestrial haulout (Slip *et al.* 1992; Wheatley 2001). Moreover, southern elephant seals are subject to an increased risk of predation by killer whales *Orcinus orca* at haulout sites (Condy *et al.* 1978; Ridoux 1986; Guinet 1991; Keith *et al.* 2001; Pistorius *et al.* 2002b; Tosh *et al.* 2008; Reisinger *et al.* 2011). The annual timing of visits by killer whales to Subantarctic islands coincides with periods of increased elephant seal activity in the vicinity of these islands (Condy *et al.* 1978; Keith *et al.* 2001). While sightings of these killer whales are most common during the elephant seal breeding season from September to December of each year, a second but smaller peak occurs in March to May when under-yearling and other elephant seals return to terrestrial habitat for their winter haulout (Voisin 1972; Condy *et al.* 1978; Guinet 1991; Keith *et al.* 2001; Reisinger *et al.* 2011).

Despite the costs, elephant seals have no choice but to be ashore during certain periods. They are born ashore and spend the first few weeks of life ashore (Laws 1956; Carrick *et al.* 1962a; Lenglart & Bester 1982; Wilkinson & Bester 1990), and must be ashore to moult. During this phase, the entire outer layer of skin and all hair is lost and thermoregulatory abilities are compromised (Slip *et al.* 1992; Worthy *et al.* 1992b; Boyd *et al.* 1993), rendering this haulout obligatory. Although there is substantial evidence that some mating does take place at sea, most is thought to take place during the breeding haulout (de Bruyn *et al.* 2011).

While all other terrestrial periods are obligatory, it is not known whether this is the case for the winter haulout. Individual animals may come ashore from one to three times per year during the winter, but some are thought to skip participation in this type of haulout in any given year (Carrick *et al.* 1962a; Wilkinson 1992; Kirkman *et al.* 2001). Despite the apparently optional nature of the winter haulout, considering the investment in time and energy, and the predation risks, the winter haulout must have a purpose. A number of possibilities have been suggested (many reviewed in Burton 1985), one of which is that repeated visits ensure greater familiarity to the natal island and therefore allow greater site fidelity during breeding haulouts as an adult (Burton 1985; Pistorius *et al.* 2002a). Pistorius et al. (2002a) found significantly higher resighting rates at the island of their birth for seals that had been recorded ashore during the winter haulout compared to those that had not.

Site fidelity in migratory animals has been shown for a number of species and is thought to be beneficial for a variety of reasons (Greenwood 1980; Bateson 1982; Shields 1987; Pusey & Wolf 1996). Elephant seals also show site fidelity (Carrick & Ingham 1962b; Nichols 1970; Campagna & Lewis 1992; Hofmeyr 2000) possibly because their own survival indicates that their natal site is a suitable breeding site (Hofmeyr 2000). Furthermore, familiarity with a site may aid seals in securing and retaining the resources required during the breeding haulout (Hofmeyr 2000). It is also possible that their return to the vicinity of a previously used site may aid them in selecting habitat suitable for raising a pup to weaning.

In this study I examined the possibility that the winter haulout serves to increase site fidelity by examining the effect that the history of participation in the winter haulout has on fidelity to individual beaches at the location of the study, Marion Island, during the breeding season. I also compared this to the history of resights of individuals during moult haulouts undertaken as immatures.

Marion Island in the Southern Ocean (46º 54' S., 37º 45' E.) supports a population of approximately 2 100 elephant seals with some 500 pups born annually (Pistorius *et al.* 2004; Pistorius *et al.* 2011). A long-term mark-recapture programme has yielded considerable data on the Marion Island elephant seal population. I used these data to examine the influence of the history of participation in the winter haulout by immature females on their later fidelity to natal sites during breeding haulouts. Given that multiparous adult female elephant seals show significant fidelity to the site of the first breeding event (Hofmeyr 2000), I assessed the site fidelity of primiparous and multiparous females separately. I attempted to answer the following questions: what portion of animals surviving to breed were recorded ashore as immatures during various haulout events; is a history of participation in the winter haulout as immature animals at the natal island associated with increased fidelity to their natal site by females returning to breed for the first time (primiparous animals); and is the history of participation in the winter haulout as immature animals associated with site fidelity of those hauling out during subsequent breeding seasons (multiparous animals)? To determine whether any relationship found between site fidelity and recorded presence ashore during the winter haulout was unique, I further investigated whether the history of resights during moult haulouts when immature was associated with natal site fidelity by both primiparous and multiparous breeding females, and whether the history of resights during all haulouts when immature, irrespective of type, was associated with natal site fidelity by both primiparous and multiparous breeding females.

Methods

Study site

Marion Island is in one of two islands in the Prince Edward Islands archipelago. Southern elephant seals haul out regularly but unevenly on 41 beaches on its north-east and east coasts, and part of the south coast of the island (Fig. 4.1). Irregular searches elsewhere indicate that very few seals come ashore outside of this area (Mulaudzi *et al.* 2008). All but two of the beaches on Marion Island are separated from neighbouring beaches by cliffs or other terrain that is generally impassable to elephant seals. Seals are required to swim among most sites and the sites can therefore be regarded as distinct entities. Distances among sites were measured as the shortest distance along the coastline from the centre of one site to another. Indentations along the coastline were ignored.

Field work

From 1983, all elephant seals born on Marion Island were marked within days of weaning at their natal site, with known exceptions in two years, estimated at 2 % and 5 % of those cohorts. All seals (9 963 individuals) were tagged with Jumbo Rototags (Dalton, Henley-on-Thames, England) in the interdigital webbing of each of their hind-flippers. A unique combination of tag colours and numbers allowed for subsequent recognition of individuals.

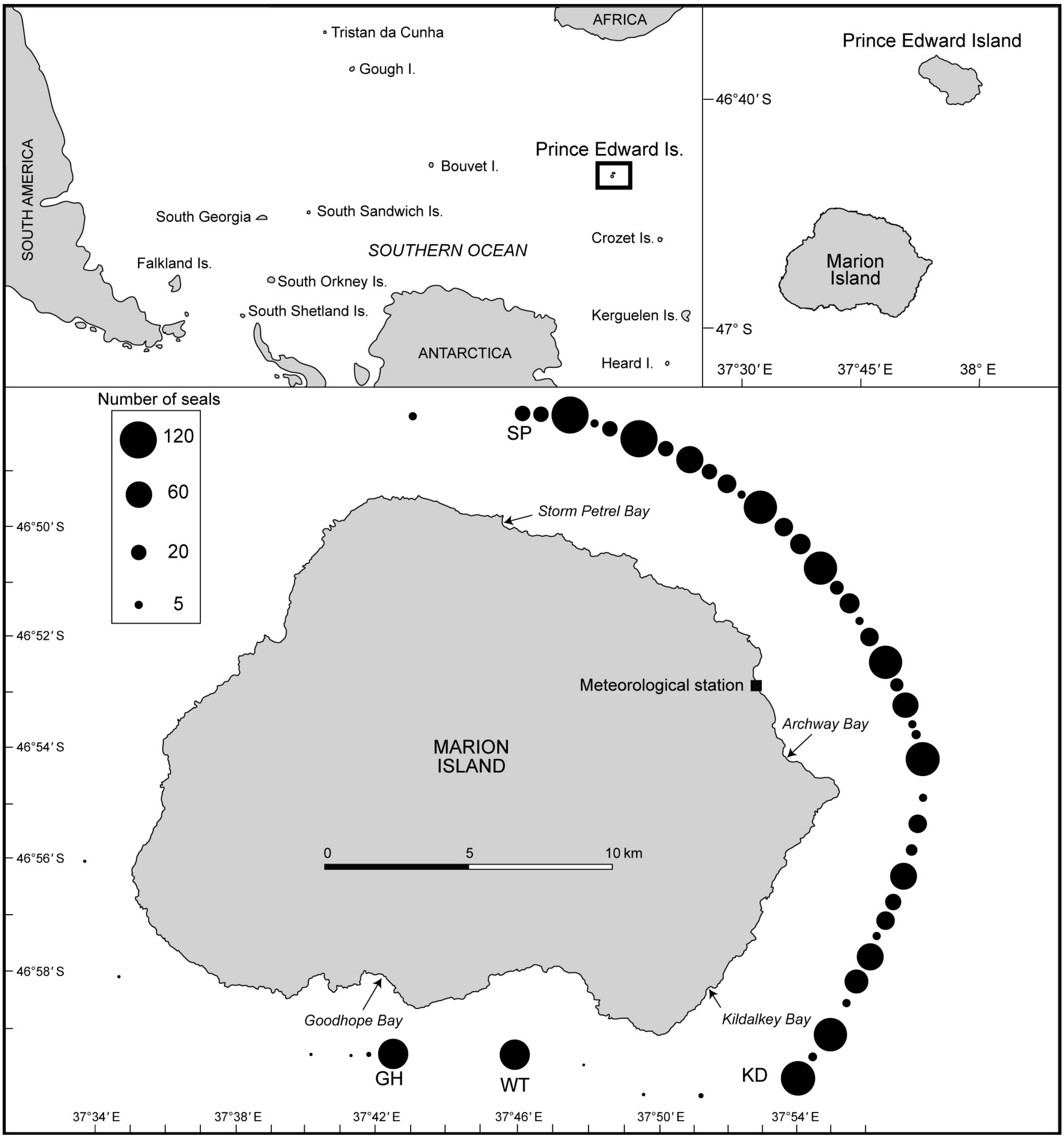

Figure 4.1 Map of Marion Island showing the distribution of southern elephant seals *Mirounga leonina*. The areas of the circles are directly proportional to the mean annual number of elephant seals hauling out at each site. The north and east sections of the coastline between locations marked SP and KD and at locations marked WT and GH form the study area. Reproduced from *African Journal of Marine Science* (2012) 34(3): 373-382 with permission © NISC (Pty) Ltd.

In association with the above, a resight programme was also initiated in 1983. This comprised systematic searches for seals ashore within the study area. Searches were conducted approximately weekly during the annual breeding haulout (August – November) and every ten days at other times of the year. Up to1990, searches of the north-east and east coast took place from September to May with monthly searches of the south coast. From 1990, these beaches were visited throughout the year, following the same pattern, and since September 1992 the southern beaches were also visited every 7 or 10 days. During these searches the haulout site, haulout type, moult status (if moulting) and breeding status (if breeding) of tagged seals were recorded, together with the identifying tag colour and number. Seals were assumed to age by one year on the peak haulout date of the breeding season (15th of October) in each year following Wilkinson (1992). Animals that had hauled out for the breeding season before the 15th of October, however, were assumed to age by a year at the start of their breeding haulout.

Data editing and analysis

The database comprised 43 029 records of tagging and resighting female seals during the period November 1983 to December 2003. Prior to analysis this database was edited in three stages:

1. Records with obvious errors (incompatible associations of data) were identified, and either corrected, or removed if they could not be corrected. This left a database of 38 917 records;
2. Each individual seal was potentially recorded multiple times during a single haulout event. To facilitate analysis, replicate records for each haulout event were discarded; single records were selected to be representative of each breeding haulout in each year

by each seal. The selected records were either (i) the first record at the location where she was sighted most often with a pup, (ii) if she was not sighted with a pup, then the first record of the location where she was sighted most often, or (iii) where she was not sighted with a pup and the number of records at different locations were equal, then the first record of the first location. The resulting database consisted of 18 936 records;

3. Immature animals are defined as those younger than three years of age (Laws 1956; Carrick *et al.* 1962b).

A number of animals may not be observed during haulouts if they have lost both tags, have been missed by observers or have hauled out elsewhere (see Pistorius *et al*. 2004 for a discussion of resighting probabilities). Therefore, only those females recorded ashore for the first time between the ages of 3 - 6 years inclusive were classified as primiparous. Records of females recorded breeding for the first time at ages older than six years were assumed to have bred elsewhere first and were discarded. Only 2.7 % of females recorded surviving to breed were recorded to breed for the first time at ages seven or older (Mammal Research Institute, unpublished data). Once a female was recorded ashore for a second breeding season, irrespective of age, she was classified as multiparous. Primiparity and multiparity was assumed and based on physiological markers.

Effects of the history of participation in winter or moult haulouts by immatures on natal site fidelity by breeding animals was assessed using two methods: by comparing frequency distributions of the distances from natal to breeding sites between animals that had and had not participated in specific haulout events; and comparing the frequency distributions of the distances from natal to breeding sites among categories of animals that were defined by the number of years that they had participated in a specific haulout type. Data were analysed using standard non-parametric tests: the Kruskal-Wallis ANOVA, with multiple comparison of ranks *post hoc* tests where significance was found, and the Kolmogorov-Smirnov Test. Significance was set at $p < 0.05$.

Results

Participation in winter and moult haulouts by immature animals at the study site

The proportion of female southern elephant seals that were recorded ashore at Marion Island when they were immature, but that survived to breed at the study site, varied with age. While between 70 and 80 % had been observed to haul out in winter or to moult as yearlings at the study site, or to moult as two-year-olds, only approximately half had been observed to winter as underyearlings and a third to winter as two-year-olds (Fig. 4.2). Approximately 85 % of females hauling out to breed as adults hauled out at least once at the study site during a winter when immature, but only 13 % were observed to

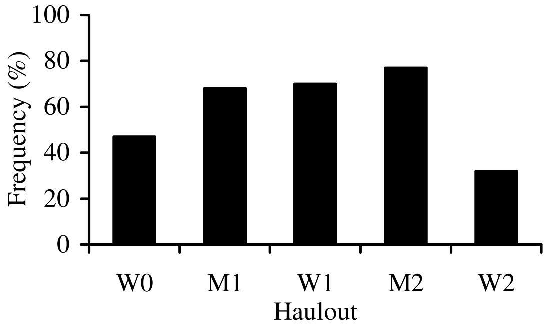

Figure 4.2 Percentage of breeding female southern elephant seals that were recorded ashore on Marion Island as immature animals during three possible winter haulouts (W0 – as underyearling, W1 – as a yearling, W2 – as two-year old) and two possible moult haulouts (M1 – as a yearling, M2 – as a two-year old).

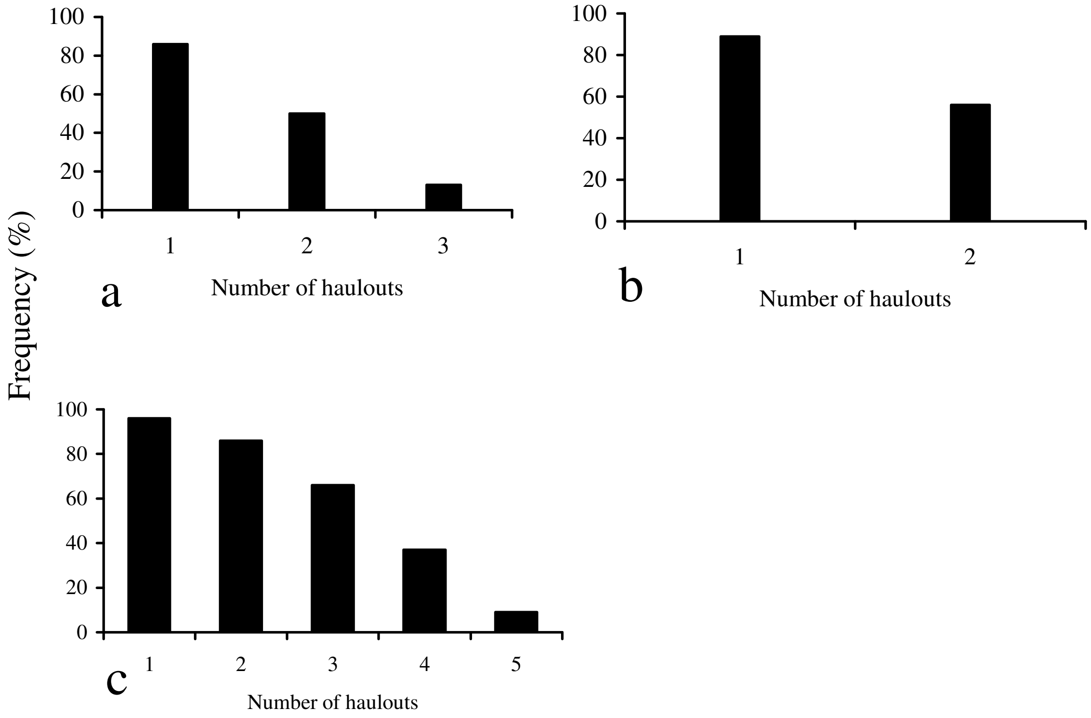

Figure 4.3 Percentage of all breeding female southern elephant seals recorded ashore as immature animals at Marion Island during (a) one, two, or all three winter haulouts, (b) one or both moult haulouts, and (c) at least one, two, three, four, or in all five haulouts.

haul out in all winter haulouts during their first three years of life (Fig. 4.3a). Over 85 % of breeding adult females were recorded to moult at least once at the study site as an immature animal (Fig. 4.3b). Only approximately half of the breeding adult females had been recorded during the moult at the study site as both yearlings and two-year-olds. A total of 96 % of breeding female southern elephant seals had been recorded ashore at least once during a winter or moult haulout as an immature, but only nine percent of breeding females had been recorded ashore during all haulouts as an immature (Fig. 4.3c).

Natal site fidelity and history of winter haulout participation of primiparous females

Females that had participated in winter haulouts at Marion Island as underyearlings (Kolmogorov-Smirnov, $n_1 = 501$, $n_2 = 626$, $p<0.025$), as yearlings (Kolmogorov-Smirnov, $n_1 = 761$, $n_2 = 365$, $p<0.005$) or as two-year-olds (Kolmogorov-Smirnov, $n_1 = 350$, $n_2 = 777$, $p<0.025$) hauled out significantly closer to their natal sites during their first breeding season than females that had not (Fig. 4.4). Furthermore, the number of winter haulouts participated in to the age of three had a significant effect on fidelity to natal site during first breeding haulout (Kruskal-Wallis ANOVA: $H_{(3,\,1126)} = 22.5$, $p < 0.001$). *Post-hoc* tests indicated that this difference lay entirely between those that had not hauled out at the study site during a winter as an immature animal and those that had hauled out once ($z = 3.2$, $p = 0.010$), twice ($z = 4.5$, $p < 0.001$) or three times previously ($z = 3.6$, $p < 0.002$) (Fig. 4.5).

Natal site fidelity and history of winter haulout participation of multiparous females

Although breeding multiparous females that had been recorded as juveniles during winter haulouts showed higher natal site fidelity than those that had not (Fig. 4.6), these differences were not significant whether the comparison was of their history as underyearlings (Kolmogorov-Smirnov, $n_1 = 840$, $n_2 = 937$, $p > 0.10$), yearlings (Kolmogorov-Smirnov, $n_1 = 1248$, $n_2 = 529$, $p > 0.10$) or two-year-olds (Kolmogorov-Smirnov, $n_1 = 569$, $n_2 = 1208$, $p > 0.10$). In addition, the number of winter haulouts participated in as an immature animal had no significant influence (Kruskal-Wallis ANOVA: $H_{(3,\,1777)} = 1.89$, $p = 0.60$) on fidelity to natal site of females hauling out to breed in years subsequent to their first breeding haulout (Fig. 4.7).

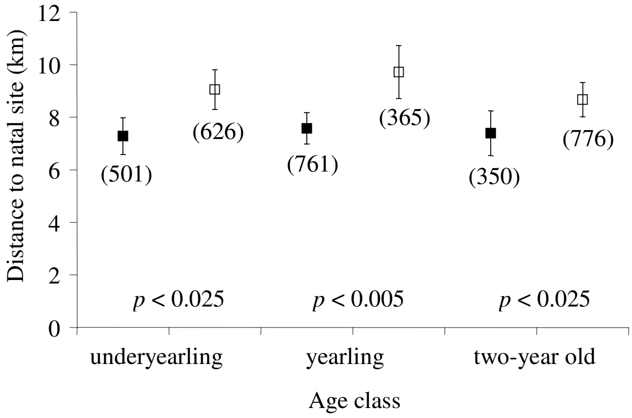

Figure 4.4 Mean distance (± 95 % confidence limits) between natal and breeding site of primiparous female southern elephant seals in relation to their history of presence or absence during specific winter haulouts at Marion Island. The age class indicated is that at which the previous haulout took place. Closed squares indicate animals that were recorded ashore during a specific event, whereas open squares indicate animals that were not recorded ashore during that event. Numbers in parentheses are sample sizes. The probability of significance is shown (Kolmagorov-Smirnov test).

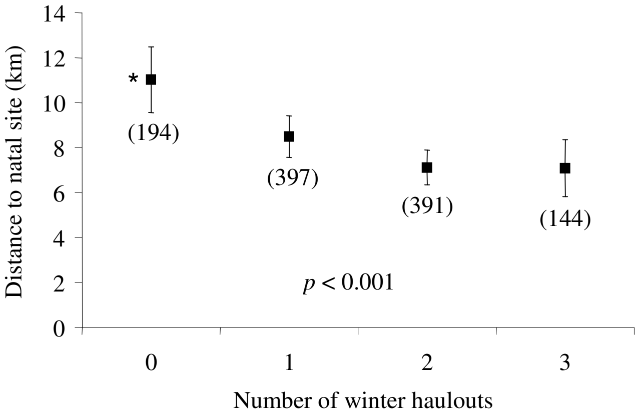

Figure 4.5 Mean distance (± 95 % confidence limits) between the natal and breeding sites of primiparous female southern elephant seals, grouped following the number of winter haulouts recorded ashore at Marion Island when immature. Numbers in parentheses are sample sizes. An asterisk marks the group that is significantly different from all others (Kruskal-Wallis ANOVA).

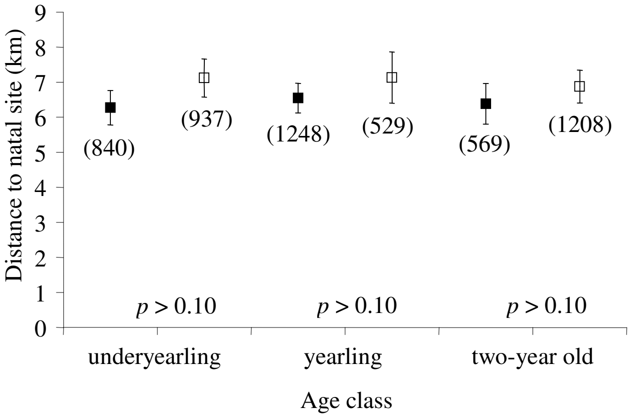

Figure 4.6 Mean distance (± 95 % confidence limits) between natal and breeding site of multiparous female southern elephant seals in relation to their history of presence or absence during specific winter haulouts at Marion Island. The age class indicated is that at which the previous haulout took place. Closed squares indicate animals that were recorded ashore during a specific event, while open squares indicate animals that were not recorded ashore during that event. Numbers in parentheses are sample sizes. The probability of significance is shown (Kolmagorov-Smirnov test).

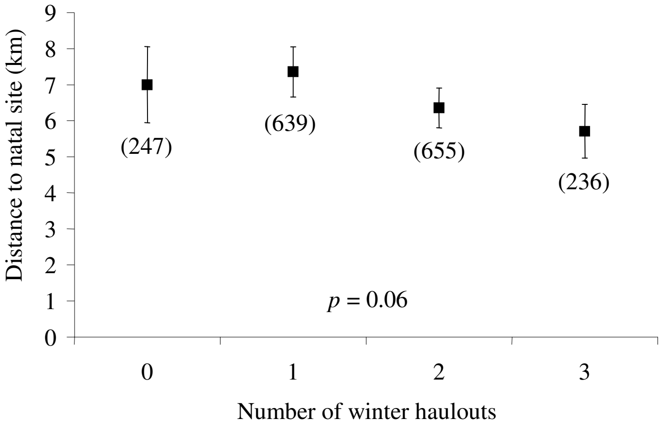

Figure 4.7 Mean distance (± 95 % confidence limits) between the natal and breeding sites of multiparous female southern elephant seals, grouped following the number of winter haulouts recorded ashore at Marion Island when immature. Numbers in parentheses are sample sizes. The probability of significance is shown (Kruskal-Wallis ANOVA).

Natal site fidelity and history of moult haulout participation of primiparous females

The record of tagged seals ashore during specific moult seasons (Fig. 4.8), indicates that those that had hauled out to moult at the study site as yearlings bred closer to their natal site than those that had not, although not significantly so (Kolmogorov-Smirnov, $n_1 = 760$, $n_2 = 367$, $p < 0.10$). Those that had hauled out to moult as two-year-olds, however, did breed significantly closer to their natal site than those that had not done so (Kolmogorov-Smirnov, $n_1 = 805$, $n_2 = 322$, $p < 0.01$). The number of moult haulouts during which individuals had been observed in the study site while immature (Fig. 4.9) had a significant influence on fidelity to natal site of breeding primiparous females (Kruskal-Wallis ANOVA: $H_{(3,\,1127)} = 17.38$, $p < 0.001$). Post-hoc tests indicated that females that had hauled out at least once ($z = 3.43$, $p < 0.002$) or twice ($z = 4.12$, $p < 0.001$) at the study site as an immature animal, bred significantly closer to their natal site the first time they hauled out to breed than those that had not hauled out at all.

Natal site fidelity and history of moult haulout participation of multiparous females

Multiparous female elephant seals that had moulted at the study site as yearlings bred significantly closer to their natal site than those that had not done so (Kolmogorov-Smirnov, $n_1 = 1207$, $n_2 = 570$, $p < 0.001$) (Fig. 4.10). Similarly, those that had moulted in the study area as two-year-olds also bred significantly closer to their natal site (Kolmogorov-Smirnov, $n_1 = 1367$, $n_2 = 410$, $p < 0.025$). The number of moult haulouts that seals were recorded to have participated in as immature animals (Fig. 4.11) also had a significant effect on their fidelity to natal site when breeding (Kruskal-Wallis ANOVA: $H_{(2,\,1777)} = 15.59$, $p < 0.001$). Multiparous seals that had been recorded to

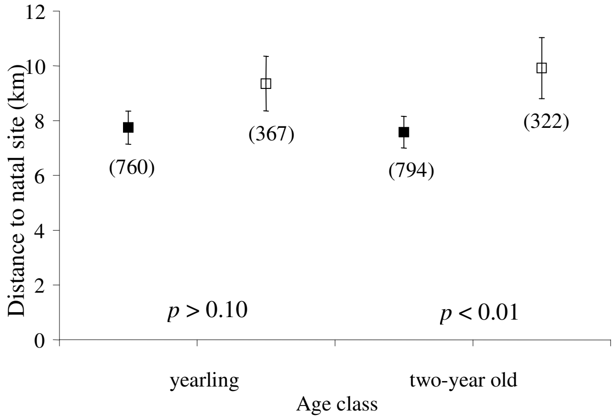

Figure 4.8 Mean distance (± 95 % confidence limits) between natal and breeding site of primiparous female southern elephant seals in relation to their history of presence or absence during specific moult haulouts at Marion Island. The age class indicated is that at which the previous haulout took place. Closed squares indicate animals that were recorded ashore during a specific event, while open squares indicate animals that were not recorded ashore during that event. Numbers in parentheses are sample sizes. The probability of significance is shown (Kolmagorov-Smirnov test).

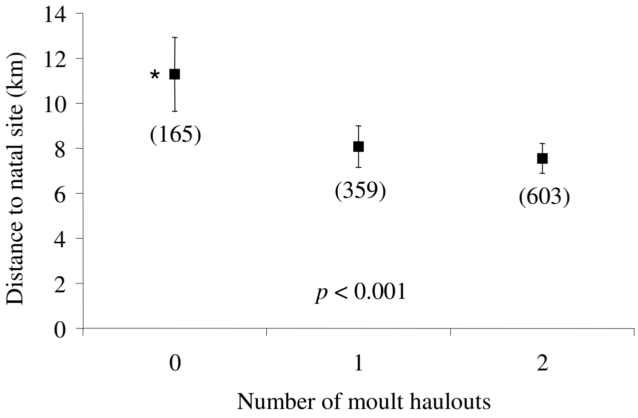

Figure 4.9 Mean distance (± 95 % confidence limits) between the natal and breeding sites of primiparous female southern elephant seals, grouped following the number of moult haulouts recorded ashore at Marion Island when immature. Numbers in parentheses are sample sizes. An asterisk marks the group that is significantly different from all others. The probability of significance is shown (Kruskal-Wallis ANOVA).

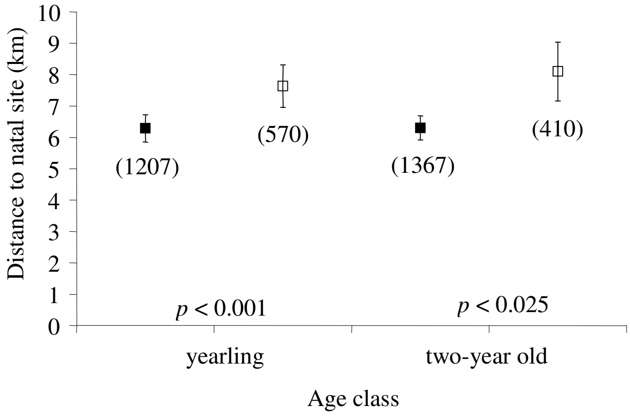

Figure 4.10 Mean distance (± 95 % confidence limits) between natal and breeding site of multiparous female southern elephant seals in relation to their history of presence or absence during specific moult haulouts at Marion Island. The age class indicated is that at which the previous haulout took place. Closed squares indicate animals that were recorded ashore during a specific event, while open squares indicate animals that were not recorded ashore during that event. Numbers in parentheses are sample sizes. The significance level is shown (Kolmagorov-Smirnov test).

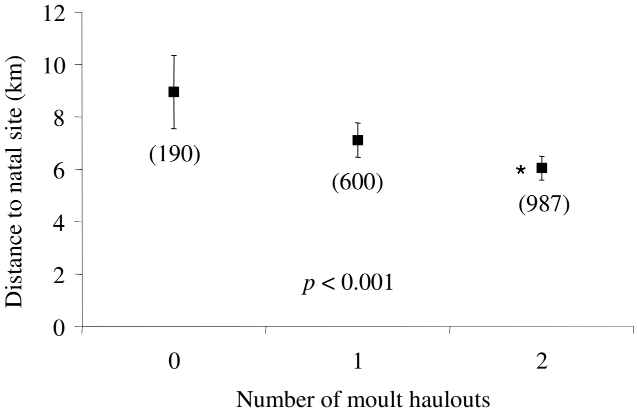

Figure 4.11 Mean distance (± 95 % confidence limits) between the natal and breeding sites of multiparous female southern elephant seals, grouped following the number of moult haulouts recorded ashore at Marion Island when immature. Numbers in parentheses are sample sizes. An asterisk marks the group that is significantly different from all others. The level of significance is shown (Kruskal-Wallis ANOVA).

moult twice in the study area as immature animals, hauled out significantly closer to their natal site to breed than those that had not been recorded ($z = 3.41$, $p = 0.002$) or recorded once only ($z = 2.75$, $p = 0.018$).

Natal site fidelity and history of participation in all haulouts of primiparous females

The fidelity to natal site by adult females hauling out to breed for the first time was significantly related to the number of times that they were recorded present during all haulouts when immature (Kruskal-Wallis ANOVA: $H_{(5,\,1127)} = 33.81$, $p < 0.001$) . Females that hauled out more often as immatures dispersed shorter distances (Fig. 4.12). Multiple comparisons *post-hoc* tests revealed a significant difference between those that were not recorded to haul out between birth and the first breeding haulout, and those that were recorded to haul out twice ($z = 4.46$, $p = 0.001$), three times ($z = 4.06$, p = 0.001), four times ($z = 5.13$, $p = 0.001$) and five times ($z = 4.17$, $p = 0.001$). There was also a significant difference between those hauling out once and those hauling out four times ($z = 3.01$, $p < 0.05$). All other *post-hoc* tests were not significant.

Natal site fidelity and history of participation in all haulouts of multiparous females

Presence or absence during haulouts as immature animals had no significant influence on later fidelity to natal site by multiparous breeding females (Kruskal-Wallis ANOVA: $H_{(5,\,1777)} = 10.49$, $p = 0.06$). Nonetheless, individuals that had hauled out as immatures tended to haul out closer to their natal sites to breed (Fig. 4.13).

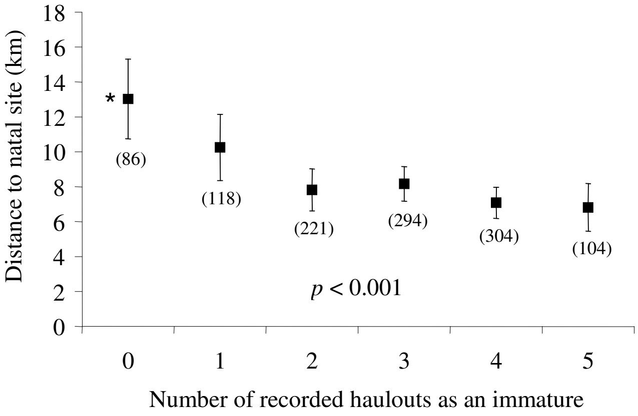

Figure 4.12 Mean distance (± 95 % confidence limits) between the natal and breeding sites of primiparous female southern elephant seals, grouped following the number of haulouts recorded ashore at Marion Island when immature. Numbers in parentheses are sample sizes. An asterisk marks the group that is significantly different from all others except group 1. The significance level is shown (Kruskal-Wallis ANOVA).

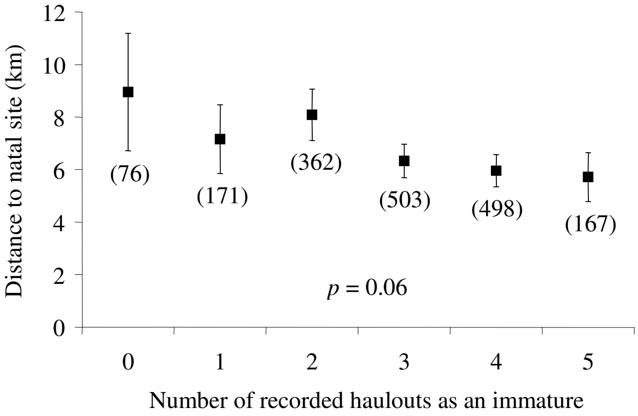

Figure 4.13 Mean distance (± 95 % confidence limits) between the natal and breeding sites of multiparous female southern elephant seals, grouped following the number of haulouts recorded ashore at Marion Island when immatures. Numbers in parentheses are sample sizes. The level of significance is shown (Kruskal-Wallis ANOVA).

Discussion

Conducting the first intensive study of a group of marked southern elephant seals, Carrick *et al*. (1962a, p. 149) stated that "The adaptive significance of virtual detachment from the sea during breeding and moulting is fairly obvious, but the autumn-winter haul-out presents a puzzle". The function of this haulout remains a puzzle (Burton 1985; Pistorius *et al.* 2002a), perhaps because it is perceived as the least important of the terrestrial phases undertaken by this species and as such has been the least examined. A number of suggestions concerning its function have been made (many reviewed in Burton 1985): the winter haulout is a resting haulout (Carrick *et al.* 1962a; Panagis 1981; Bester 1989; Ling & Bryden 1992), allowing animals to conserve energy (Burton 1985); it allows immature animals to digest food (Matthews 1952); it allows the strengthening of dentine to take place (Carrick *et al.* 1962a; Carrick & Ingham 1962a); it is a training period for terrestrial activities and allows physiological conditioning of the body to later terrestrial periods (Carrick *et al.* 1962a); it allows immature animals to avoid competing with adults for food resources (Burton 1985); and repeated visits ensure greater familiarity to the natal island and therefore allow greater site fidelity during breeding haulouts as an adult (Burton 1985; Pistorius *et al.* 2002a). Whereas this last hypothesis is the major focus of this chapter, evidence for the other suggestions is briefly discussed.

Of the abovementioned hypotheses, the most widely accepted is that the winter haulout allows the animals to rest. Resting implies conserving energy, but when one considers the amount of energy that would be required to cover the vast distances between foraging locations and terrestrial haulouts (Hindell & Burton 1988; Bester &

Pansegrouw 1992a; Jonker & Bester 1998; Field *et al.* 2001; Biuw *et al.* 2007; Tosh *et al.* 2009; Bailleul *et al.* 2010) this hypothesis seems implausible. It is possible, however, that those animals feeding in the vicinity of a haulout site during the winter come ashore to rest. Wheatley (2001) noted that immature female elephant seals with a lower weaning mass were more likely to be recorded ashore during the winter. Possibly these animals were unable to sustain long periods at sea.

Related to the above is the hypothesis that young animals come ashore to digest food. Pinnipeds, including southern elephant seals, however, have digestive rates (consumption to defecation) of less than 24 hours (Markussen 1993; Krockenberger & Bryden 1994). Therefore, the duration of a winter haulout of several weeks is far longer than is necessary. Furthermore, as Carrick *et al*. (1962a) have noted, it is implausible that much digestion will take place on land due to the substantial distances between foraging locations and the haulout site. Whereas elephant seals of different age classes show differences in foraging behaviour (Lewis *et al.* 2006; McIntyre *et al.* 2010) and it is therefore possible that immatures feed closer to Marion Island than adults, immature elephant seals hauling out at Macquarie Island fed at sites distant from that island (Van den Hoff *et al.* 2002; Field *et al.* 2005).

Carrick and Ingham (1962a) suggested that the winter haulout allows the hardening of dentine. They noted that the physiological demands of continual deep diving on immature animals may affect the growth of teeth, especially since the dive response reduces a number of physiological activities. This may be particularly important for males, as they grow larger teeth than females. They also mature later than females (Laws 1956) and participate in winter haulouts for more years than females (Kirkman *et* *al.* 2001). Whereas the hardening of dentine theory is plausible, many elephant seals are thought not to haul out during the winter (Kirkman *et al.* 2001). A related suggestion is that the winter haulout is that it is a physiological conditioning period (Carrick *et al.* 1962a; Burton 1985). It is possible that the physiological demands of the moult haulout (Slip *et al.* 1992; Worthy *et al.* 1992a; Boyd *et al.* 1993) inhibit the required levels of conditioning during such haulouts. Wheatley (2001), however, noted no difference in at-sea mass gain, moult mass loss rate or body composition of immatures during the moult whether they were recorded ashore during the previous winter or not.

Burton (1985) suggested that by hauling out during the winter, immature animals avoid competition with adults. During this time adults of both sexes feed in preparation for the energetically taxing breeding season (Reiter & Le Boeuf 1991; Boyd *et al.* 1994; Arnbom *et al.* 1997). The winter is therefore likely to be a particularly competitive foraging period. Significant competition among animals of various ages and age–sex classes is indicated by some separation in foraging areas (Bornemann *et al.* 2000; McConnell *et al.* 2002; Field *et al.* 2004, 2005) and differences in diet (Field *et al.* 2007).

Pistorius *et al*. (2002a) suggested that the winter haulout may serve to increase site fidelity of southern elephant seals by facilitating familiarity with the natal island. In support of this they found that the probability of resighting animals at their natal island increased if they had been present during at least one winter haulout when immature. My results support their findings for primiparous but not for multiparous females. I have further shown that the relationship between winter haulouts and natal site fidelity is evident not only for the natal island, as demonstrated by Pistorius et al. (2002a), but also at a finer hierarchical level, to that of individual natal beaches. I also found, however, that greater fidelity was linked not only to recorded presence during winter haulouts as immature animals, but also to recorded presence during moult haulouts as immature animals, and in fact to their presence during all haulouts of immature animals at the study site. Moreover I found that, whereas natal site fidelity by multiparous females was not linked to their recorded presence ashore during winter haulouts, it is significantly linked to recorded presence ashore during moult haulouts when immature.

The implications of these findings are that, whereas participation in the winter haulout may facilitate greater familiarity with the natal site, this might not be the sole reason, or even a reason at all, for the existence of the winter haulout, considering that presence ashore during the moult haulout also facilitates greater natal site fidelity. In fact the results indicate that, while site fidelity of primiparous females is increased by at least one visit to the natal island as an immature, further visits and the type of visit may not be important in terms of increasing site fidelity. The purpose of the winter haulout remains unknown.

The lack of an association between natal site fidelity of multiparous breeding females and their recorded presence or absence during winter haulouts is possibly due to the greater duration of the period since these visits. Hofmeyr (2000) found that younger primiparous females at Marion Island showed greater natal site fidelity than older primiparous females. While it is not known which navigational cues are used by seals to locate a haulout site, it is possible that memories of a previously visited site fade with time.

Of female elephant seals born on Marion Island and later recorded to breed there, some 30 % were not recorded moulting in the study area as yearlings, and 20 % were not recorded moulting as two-year olds. Given that an annual moult haulout is thought to be obligatory (Slip *et al.* 1992; Worthy *et al.* 1992b; Boyd *et al.* 1993), it is likely that the absent animals moulted elsewhere. Bester & Hofmeyr (2005) and Oosthuizen et al. (2009) recorded tagged immature elephant seals moulting on neighbouring Prince Edward Island, whereas Bester (1989) and Oosthuizen *et al*. (2011) recorded the movement of tagged seals from their natal island to moult sites elsewhere, among Marion Island, Île de la Possession in the Crozet Archipelago, and Îles Kerguelen. These percentages of animals not recorded during the moult are similar to the percentages of these age classes not recorded during the winter haulout at the study site by yearlings. Although the winter haulout has been considered to be optional (Carrick *et al.* 1962a; Wilkinson 1992; Kirkman *et al.* 2001), it is possible (as immature animals must moult elsewhere when they are not recorded at the study site) that immature animals also do not miss a winter haulout either, at least not as underyearlings and yearlings, hauling out on neighbouring or more distant islands when they are not recorded on their natal island. To further address the questions posed by the winter haulout, some idea of the levels of participation in this haulout is required. Fitting a suitable sample of immature animals with satellite tags of sufficient battery duration should provide valuable data in this regard.

References

ARNBOM, T., FEDAK, M.A. & BOYD, I.L. 1997. Factors affecting maternal expenditure in southern elephant seals during lactation. *Ecology* **78:** 471-483.

BAILLEUL, F., COTTÉ, C. & GUINET, C. 2010. Mesoscale eddies as foraging area of a deep-diving predator, the southern elephant seal. *Marine Ecology Progress Series* **408:** 251-264.

BATESON, P.P.G. 1982. Preferences for cousins in Japanese quail. *Nature* **295:** 236-237.

BESTER, M.N. 1989. Movements of southern elephant seals and Subantarctic fur seals in relation to Marion Island. *Marine Mammal Science* **5:** 257-265.

BESTER, M.N. & HOFMEYR, G.J.G. 2005. Numbers of elephant seals at Prince Edward Island, Southern Ocean. *South African Journal of Wildlife Research* **35:** 85-88.

BESTER, M.N. & PANSEGROUW, H.M. 1992a. Ranging behaviour of southern elephant seal cows from Marion Island. *South African Journal of Science* **88:** 574-577.

BESTER, M.N. & PANSEGROUW, H.M. 1992b. Ranging behaviour of southern elephant seal cows from Marion Island. *South African Journal of Science* **88:** 574-575.

BIUW, M., BOEHME, L., GUINET, C., HINDELL, M.A., COSTA, D., CHARRASSIN, J.-B., ROQUET, F., BAILLEUL, F., MEREDITH, M., THORPE, S., TREMBLAY, Y., MCDONALD, B., PARK, Y.-H., RINTOUL, S.R., BINDOFF, N., GOEBEL, M., CROCKER, D., LOVELL, P., NICHOLSON, J., MONKS, F. & FEDAK, M.A. 2007. Variations in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. *Proceedings of the National Academy of Sciences* **104:** 13705-13710.

BORNEMANN, H., KREYSCHER, M., RAMDOHR, S., MARTIN, T., CARLINI, A., SELLMANN, L. & PLÖTZ, J. 2000. Southern elephant seal movements and Antarctic sea ice. *Antarctic Science* **12:** 3-15.

BOYD, I.L., ARNBOM, T. & FEDAK, M.A. 1993. Water flux, body composition and metabolic rate during molt in female southern elephant seals (*Mirounga leonina*). *Physiological Zoology* **66:** 43-60.

BOYD, I.L., ARNBOM, T.A. & FEDAK, M.A. 1994. Biomass and energy consumption of the South Georgia population of southern elephant seals. In: *Elephant seals: population ecology, behavior and physiology*, (ed) B.J. Le Boeuf & R.M. Laws, pp. 98-117. University of California Press Berkeley.

BURTON, H.R. 1985. Tagging studies of male southern elephant seals (*Mirounga leonina* L.) in the Vestfold Hills area, Antarctica, and some aspects of their behaviour. In: *Studies of Sea Mammals in South Latitudes*, (ed) J.K. Ling & M.M. Bryden, pp. 19-30. Geographic Services (Pty) Ltd., Adelaide.

CAMPAGNA, C. & LEWIS, M. 1992. Growth and distribution of a southern elephant seal colony. *Marine Mammal Science* **8:** 387-396.

CARRICK, R., CSORDAS, S.E., INGHAM, S.E. & KEITH, K. 1962a. Studies of the southern elephant seal, *Mirounga leonina* (L.). III. The annual cycle in relation to age and sex. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 119-160.

CARRICK, R., CSORDAS, S.E., INGHAM, S.E. & KEITH, K. 1962b. Studies on the southern elephant seal, *Mirounga leonina* (L.). III. The annual cycle in relation to age and sex. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 119-160.

CARRICK, R. & INGHAM, S.E. 1962a. Studies on the southern elephant seal *Mirounga leonina* (L.). II. Canine tooth structure in relation to function and age determination *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 102-126.

CARRICK, R. & INGHAM, S.E. 1962b. Studies on the southern elephant seal, *Mirounga leonina* (L.) V. Population dynamics and utilization. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 198-206.

CONDY, P.R. 1979. Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.) at Marion Island. *South African Journal of Zoology* **14:** 95-102.

CONDY, P.R., VAN AARDE, R.J. & BESTER, M.N. 1978. The seasonal occurrence and behaviour of killer whales *Orcinus orca*, at Marion Island. *Journal of Zoology, London* **184:** 449-464.

DE BRUYN, P.J.N., TOSH, C.A., BESTER, M.N., CAMERON, E.Z., MCINTYRE, T. & WILKINSON, I.S. 2011. Sex at sea: alternative mating system in an extremely polygynous mammal. *Animal Behaviour* **82:** 445-451.

FIELD, I., HINDELL, M.A., SLIP, D.J. & MICHAEL, K.J. 2001. Foraging strategies of southern elephant seals (*Mirounga leonina*) in relation to frontal zones and water masses. *Antarctic Science* **13:** 371-379.

FIELD, I.C., BRADSHAW, C.J.A., BURTON, H.R. & HINDELL, M.A. 2004. Seasonal use of oceanographic and fisheries management zones by juvenile southern elephant seals (*Mirounga leonina*) from Macquarie Island. *Polar Biology* **27:** 432-440.

FIELD, I.C., BRADSHAW, C.J.A., BURTON, H.R. & HINDELL, M.A. 2005. Juvenile southern elephant seals exhibit seasonal differences in energetic requirements and use of lipids and protein stores. *Physiological and Biochemical Zoology* **78:** 491-504.

FIELD, I.C., BRADSHAW, C.J.A., VAN DEN HOFF, J., BURTON, H.R. & HINDELL, M.A. 2007. Age-related shifts in the diet composition of southern elephant seals expand overall foraging niche. *Marine Biology* **150:** 1441-1452.

GREENWOOD, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* **28:** 1140-1162.

GUINET, C. 1991. L'orque (*Orcinus orca*) authour de l'archipel Crozet comparaison avec d'autres localites. *Revue de Ecologie (Terre at la Vie)* **46:** 321-337.

HINDELL, M.A. & BURTON, H.R. 1988. The history of the elephant seal industry at Macquarie Island and an estimate of the pre-sealing numbers. *Papers and Proceedings of the Royal Society of Tasmania* **122:** 159-168.

HOFMEYR, G.J.G. 2000. Dispersal and dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. M.Sc., University of Pretoria, Pretoria.

JONKER, F.C. & BESTER, M.N. 1998. Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island. *Antarctic Science* **10:** 21-30.

KEITH, M., BESTER, M.N., BARTLETT, P.A. & BAKER, D. 2001. Killer whales (*Orcinus orca*) at Marion Island, Southern Ocean. *African Zoology* **36:** 163-175.

KIRKMAN, S.P., BESTER, M.N., PISTORIUS, P.A., HOFMEYR, G.J.G., OWEN, R. & MECENERO, S. 2001. Participation in the winter haulout by southern elephant seals (*Mirounga leonina*). *Antarctic Science* **13:** 380-384.

KROCKENBERGER, M.B. & BRYDEN, M.M. 1994. Rate of passage of digesta through the alimentary tract of southern elephant seals (*Mirounga leonina*) (Carnivora: Phocidae). *Journal of Zoology, London* **234:** 229-237.

LAWS, R.M. 1956. The elephant seal (*Mirounga leonina* Linn.). II. General social and reproductive behaviour. *Falkland Islands Dependencies Survey Scientific Reports* **13:** 1-88.

LAWS, R.M. 1993. Identification of species. In: *Antarctic seals: research methods and techniques*, (ed) R.M. Laws, pp. 1-28. Cambridge University Press, Cambridge.

LE BOEUF, B.J. & LAWS, R.M. 1994. Elephant seals: an introduction to the genus. In: *Elephant seals: population ecology, behavior and physiology*, (ed) B.J. Le Boeuf & R.M. Laws, pp. 1-26. University of California Press, Berkeley.

LENGLART, P.Y. & BESTER, M.N. 1982. Post-weaning dispersion of southern elephant seal *Mirounga leonina* underyearlings at Kerguelen. *Revue d'Écologie (Terre et la Vie)* **36:** 175-186.

LEWIS, R., O'CONNELL, T.C., LEWIS, M., CAMPAGNA, C. & HOELZEL, A.R. 2006. Sex-specific foraging strategies and resource partitioning in the southern elephant seal (*Mirounga leonina*). *Proceedings of the Royal Society, Series B* **273:** 2901-2907.

LING, J.K. & BRYDEN, M.M. 1992. *Mirounga leonina*. *Mammalian Species* **391:** 1-8.

MARKUSSEN, N.H. 1993. Transit time of digesta in captive harbour seals (*Phoca vitulina*). *Canadian Journal of Zoology* **71:** 1071-1073.

MATTHEWS, L.H. 1952. *Sea elephant: the life and death of the elephant seal.* MacGibbon and Kee, London. 190 pp.

MCCONNELL, B., FEDAK, M.A., BURTON, H.R., ENGELHARD, G.H. & REIJNDERS, P.J.H. 2002. movements and foraging areas of naïve recently weaned southern elephant seal pups. *Journal of Animal Ecology* **71:** 65-78.

MCINTYRE, T., BORNEMANN, H., PLÖTZ, J., TOSH, C.A. & BESTER, M.N. 2011. Water column use and forage strategies of female southern elelphant seals from Marion Island. *Marine Biology* **158:** 2125-2139.

MCINTYRE, T., DE BRUYN, P.J.N., ANSORGE, I.J., BESTER, M.N., BORNEMANN, H., PLÖTZ, J. & TOSH, C.A. 2010. A lifetime at depth: vertical distribution of southern elephant seals in the water column. *Polar Biology* **33:** 1037-1048.

MULAUDZI, T.W., HOFMEYR, G.J.G., BESTER, M.N., KIRKMAN, S.P., PISTORIUS, P.A., JONKER, F.C., MAKHADO, A.B., OWEN, J.H. & GRIMBEEK, R.J. 2008. Haulout site selection by southern elephant seals at Marion Island. *African Zoology* **43:** 25-33.

NICHOLS, D.G. 1970. Dispersal and dispersion in relation to the birthsite of the southern elephant seal, *Mirounga leonina* (L.), of Macquarie Island *Mammalia* **34:** 598-616.

OOSTHUIZEN, W.C., BESTER, M.N., DE BRUYN, P.J.N. & HOFMEYR, G.J.G. 2009. Intra-archipelago moult dispersion of southern elephant seals at the Prince Edward Islands, southern Indian Ocean. *African Journal of Marine Science* **31:** 457-462.

OOSTHUIZEN, W.C., BESTER, M.N., TOSH, C.A., GUINET, C., BESSON, D. & DE BRUYN, P.J.N. 2011. Dispersal and dispersion of southern elephant seals in the Kerguelen province, Southern Ocean. *Antarctic Science* **23:** 567-577.

PANAGIS, K. 1981. Local movement of southern elephant seal pups *Mirounga leonina* (Linn.) at Marion Island. *South African Journal of Antarctic Research* **10/11:** 28-31.

PISTORIUS, P.A., BESTER, M.N., LEWIS, M.N., TAYLOR, F.E., CAMPAGNA, C. & KIRKMAN, S.P. 2004. Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal (*Mirounga leonina*). *Journal of Zoology, London* **263:** 107-119.

PISTORIUS, P.A., DE BRUYN, P.J.N. & BESTER, M.N. 2011. Population dynamics of southern elephant seals: a synthesis of three decades of demographic research at Marion Island. *South African Journal of marine Science* **33:** 523-534.

PISTORIUS, P.A., KIRKMAN, S.P., BESTER, M.N. & TAYLOR, F.E. 2002a. Implications of the winter haulout for future survival and resighting probablity of southern elephant seals at Marion Island. *South African Journal of Wildlife Research* **32:** 59-63.

PISTORIUS, P.A., TAYLOR, F.E., LOUW, C., HANISE, B., BESTER, M.N., DE WET, C., DU PLOOY, A., GREEN, N., KLASEN, N., PODILE, S. & SCHOEMAN, J. 2002b. Distribution, movement, and estimated population size of killer whales at Marion Island, December 2000. *South African Journal of Wildlife Research* **32:** 1-7.

PUSEY, A.E. & WOLF, M. 1996. Inbreeding avoidance in animals. *Trends in Ecology and Evolution* **11:** 201-206.

REISINGER, R.R., DE BRUYN, P.J.N. & BESTER, M.N. 2011. Predatory impact of killer whales on pinniped and penguin populations at the Subantarctic Prince Edward Islands: fact and fiction. *Journal of Zoology, London* **285:** 1-10.

REITER, J. & LE BOEUF, B.J. 1991. Life history consequences of variation in age at primiparity in northern elephant seals. *Behavioral Ecology and Sociobiology* **28:** 153-160.

RIDOUX, V. 1986. Feeding association between seabirds and killer whales, *Orcinus orca*, around subantarctic Crozet Islands. *Canadian Journal of Zoology* **65:** 2113-2115.

SHIELDS, W.M. 1987. Dispersal and mating systems: investigating their causal connections. In: *Mammalian dispersal patterns: the effects of social structure on population genetics*, (ed) B.D. Chepko-Sade & Z.T. Halpin, pp. 3-24. University of Chicago Press, Chicago.

SLIP, D.J., GALES, N.J. & BURTON, H.R. 1992. Body-mass loss, utilization of blubber and fat, and energetic requirements of male southern elephant seals, *Mirounga leonina*, during the molting fast. *Australian Journal of Zoology* **40:** 235-243.

TOSH, C.A., BORNEMANN, H., RAMDOHR, S., SCHRÖDER, M., MARTIN, T., CARLINI, A., PLÖTZ, J. & BESTER, M.N. 2009. Adult male southern elephant seals from King George Island utilize the Weddell Sea. *Antarctic Science* **21:** 113-121.

TOSH, C.A., DE BRUYN, P.J.N. & BESTER, M.N. 2008. Preliminary analysis of the social structure of killer whales, *Orcinus orca*, at subantarctic Marion Island. *Marine Mammal Science* **24:** 929-940.

VAN DEN HOFF, J., BURTON, H.R., HINDELL, M.A., SUMNER, M.D. & MCMAHON, C.R. 2002. Migrations and foraging of juvenile southern elephant seals from Macquarie Island within CCAMLR managed areas. *Antarctic Science* **14:** 134-145.

VOISIN, J.-F. 1972. Notes on the behaviour of the killer whale, *Orcinus orca* (L.). *Norwegian Journal of Zoology* **20:** 93-96.

WHEATLEY, K.E. 2001. Behavioural and physiological aspects of the mid-year haul-out for southern elephant seals (*Mirounga leonina*) on Macquarie Island. M.Phil., St. Andrews University, Aberdeen.

WILKINSON, I.S. 1992. Factors affecting reproductive success of southern elephant seals, *Mirounga leonina*, at Marion Island. Ph.D., University of Pretoria, Pretoria.

WILKINSON, I.S. & BESTER, M.N. 1990. Duration of post-weaning fast and local dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. *Journal of Zoology, London* **222:** 591-600.

WORTHY, G.A.J., MORRIS, P.A., COSTA, D.P. & LE BOEUF, B.J. 1992a. Moult energetics of the northern elephant seal (*Mirounga angustirostris*). *Journal of Zoology, London* **227:** 257-265.

WORTHY, G.A.J., MORRIS, P.A., COSTA, D.P. & LE BOEUF, B.J. 1992b. Moult energetics of the northern elephant seal (*Mirounga angustirostris*). *Journal of Zoology, London* **227:** 257.

Chapter 5 ▪ Do elephant seals forget? Loss of familiarity with terrestrial haulout sites over time.

Does the duration of the period between visits to a site and the number of visits to a site affect fidelity to that site?

Southern elephant seal breeding aggregation, Funk Bay, Marion Island. Photo – G. Hofmeyr

"Their awkward progression on land was so slow that they could easily be avoided, and one was perfectly safe unless one slipped and fell in their track; but the interesting thing was that, if you walked round behind them, they immediately forgot your existence, and lay down to sleep or make love in a sluggish but apparently satiating way: it took another stone to raise them again in surprised realization of one's existence. I think it unlikely that any animal psychologist studying memory has ever experimented with these beasts, but, when he does, I can promise him an all-time low level of retentiveness."

Robert Blackwood Robertson (1956)

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Do elephant seals forget? Loss of familiarity with terrestrial haulout sites over time.

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CHAPTER 5

DO ELEPHANT SEALS FORGET? LOSS OF FAMILIARITY WITH TERRESTRIAL HAULOUT SITES OVER TIME.

Abstract

Migratory animals benefit from returning to their natal or first breeding site. One of the factors affecting the accuracy of return to a prior site is spatial memory. It is thought that absence from a site leads to deterioration of familiarity with the location of that site. It is possible that return visits by immature animals maintain a level of spatial memory. We examined the effect of the possible loss of familiarity with a site over time, on the fidelity to that site of a migratory marine predator, the southern elephant seal *Mirounga leonina*. A shorter length of absence from a site, and a greater number of visits to a site, were associated with greater fidelity to the natal site by both breeding and moulting female seals. Furthermore, a greater number of visits to the first breeding site was associated with greater fidelity to that site when the seals returned to breed again. While the same trends were seen for males, they were mostly not significant, possibly due to a smaller sample size. While most immature elephant seals do not show strict philopatry, for any one of a number of possible reasons, their experience is linked to levels of fidelity shown later in life. This study therefore indicates the advantages of experience in maintaining site fidelity. Although there is evidence that a number of species show deterioration in spatial memory over time, to the best of our knowledge this is the first study for which this question is the primary aim. However, there are alternative explanations for the patterns shown.

Keywords: dispersal, site fidelity, memory, southern elephant seal, *Mirounga leonina*

Introduction

The dynamics of dispersal are different for sedentary and migratory animals. While sedentary animals expend energy moving away from their natal or other site, migratory animals expend energy if they attempt to return to their natal or other previously visited site (Morton 1992). Migratory animals benefit from returning to a previously used site, such as their natal site, in a number of ways: (1) familiarity with that site aids in obtaining resources and avoiding dangers, (2) they have greater assurance that that site will contain suitable habitat compared to surrounding areas, and (3) they have a greater assurance of finding mates at that site (Pärt 1990, 1991; Morton 1992; Pärt 1995; Paradis *et al.* 1998; Robertson & Cooke 1999; Dauchin & Cam 2002; Doligez & Pärt 2008). Furthermore, an animal's own survival and breeding is an indication that a previously used site is a good breeding site (Pärt 1991; Morton 1992; Paradis *et al.* 1998). Evidence exists of the greater survival and improved reproductive output in some species of migrants for individuals showing site fidelity compared to those that do not (Dow & Fredga 1983; Gauthier 1990; Pärt 1990, 1991, 1994; Dauchin & Cam 2002; MacDougall-Shackleton *et al.* 2002; Pravosudov *et al.* 2006; Doligez & Pärt 2008). This is, however, not supported by all studies (Lewis 1995; Lindberg & Sedinger 1997).

One of the factors possibly affecting accuracy of return to a previous site is spatial memory (Healy *et al.* 1996; Mettke-Hofmann & Gwinner 2003; Pravosudov *et al.*

2006). Evidence indicates that spatial memory deteriorates over time (Balda & Kamil 1989; Morton 1992; Winter & Stich 2005) and that the longer the duration of absence from a site, the less familiar an animal is with the location of that site. Return visits to a site between birth and breeding might serve to maintain familiarity with that site (Pärt 1991; Morton 1992; Pärt 1995). In this study we examined evidence for the deterioration of spatial memory over time. Specifically we examined the effect of return visits on spatial memory and whether the duration since the last visit, and the number of prior visits, was significant in the deterioration of spatial memory. To do this we assessed the possible loss of familiarity with natal and first breeding site of a migratory marine predator, the southern elephant seal *Mirounga leonina* by assessing the duration of time between the last visit to those sites and the number of times that seals had visited sites.

Southern elephant seals are sexually dimorphic polygynous marine predators (Laws 1993). They inhabit the waters of the Southern Ocean, migrating several thousand kilometres twice annually between pelagic foraging grounds and isolated subantarctic haulouts (Bester & Pansegrouw 1992; Jonker & Bester 1998). They experience four types of terrestrial periods during the course of their lives. Southern elephant seals are born ashore during the natal period in spring, and remain ashore for three weeks during lactation, and up to a month post weaning. As immature animals they frequently haul out one to three times during the autumn and winter in a terrestrial period that we will term the winter haulout. Elephant seals of all ages undergo an annual moult haulout of approximately a month’s duration during the spring and summer. The breeding haulout takes place during the spring when adult females come ashore for a month and adult males, between one and three months (Laws 1956; Carrick *et al.* 1962; Condy 1979;

Hindell 1991; Kirkman *et al.* 2003; Kirkman *et al.* 2004). At the study site, most females first haul out to breed at three to six years of age (de Bruyn 2009), whereas most males first breed at ages six to eight years (Mammal Research Institute unpublished data). During terrestrial haulouts, elephant seals seldom go to sea except into the shallows for very limited periods.

While southern elephant seals do move among islands and island groups (Bester 1989; Hindell & McMahon 2000; Van den Hoff 2001; Oosthuizen *et al.* 2009; Reisinger & Bester 2010), they also show fidelity to the natal and other terrestrial sites (Carrick & Ingham 1962; Nichols 1970; Hindell & Little 1988; Campagna & Lewis 1992; Van den Hoff 2001; Fabiani *et al.* 2006). At the study site, many seals haul out significantly closer to their natal site than expected throughout their lives and significantly closer to their first reproductive haulout site (RH1 site) as adults (Hofmeyr 2000). However, as immature animals they show greater fidelity to recent haulout sites than to their natal site. This changes when they first haul out to breed, when they haul out closest to their natal site, although not significantly closer to this site than to some recently visited sites (see Chapters 2 and 3). However, older incipient breeders disperse further from their natal site than younger animals, possibly because of a greater decline in spatial memory (Hofmeyr 2000). Pistorius *et al.* (2002) suggested that winter visits by immature seals to the area of their natal site assist them in retaining familiarity with this environment. Evidence in Chapter 4 indicates that this is possible. In this chapter I consider the evidence for a decline in spatial memory over time.

We asked a number of questions during this study. Specifically, does the passage of time and the number of visits affect the spatial memory of elephant seals as measured by the accuracy of their return to:

(1) Their natal site when they first haul out to breed?

(2) Their RH1 site when they return to breed?

(3) Their natal site when they haul out to moult?

Methods

Study site

The study site, Marion Island (46°54' S, 37°45' E), is one of two islands in the Prince Edwards Island Archipelago. Data were collected in the Extended Study Area (ESA) which forms part of the coastline of Marion Island (Figure 5.1). During their terrestrial phase southern elephant seals are almost entirely limited to this section of the coastline with very few hauling out elsewhere on the island due to an absence of suitable haulout sites (Mulaudzi *et al.* 2008). Some 500 pups are born annually, indicating a total population of approximately 2 100 animals (Pistorius *et al.* 2004; Pistorius *et al.* 2011). Elephant seals haul out unevenly at the 40 sites within the ESA. These sites isolated from each other by terrain impassable to elephant seals. Each site can therefore be regarded as a naturally discrete unit. We calculated distances among sites by measuring the shortest distance along the coastline between the centres of sites.

Fieldwork

An ongoing long-term mark-recapture programme, started in 1983, has been responsible for collecting the data analysed in this study. All the authors have spent a minimum of two years participating in this fieldwork. Twenty one cohorts, comprising almost all

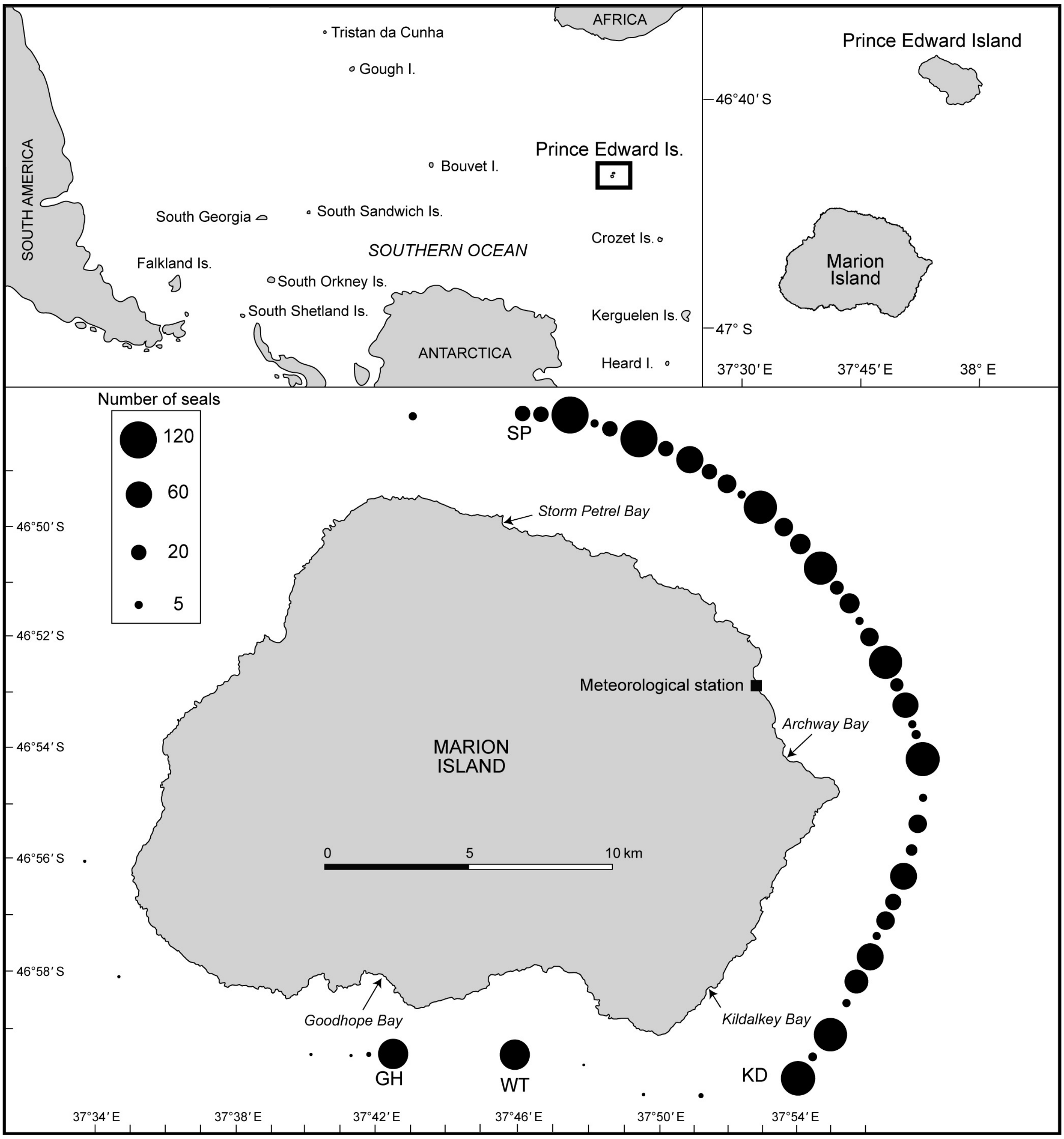


Figure 5.1 Map of Marion Island showing the distribution of southern elephant seals *Mirounga leonina*. The areas of the circles are directly proportional to the mean annual number of elephant seals hauling out at each site. The north and east sections of the coastline between locations marked SP and KD and at locations marked WT and GH form the study area. Reproduced from *African Journal of Marine Science* (2012) 34(3): 373-382 with permission © NISC (Pty) Ltd.

pups born in the ESA from 1983 to 2003 (9 963), were tagged at their natal site shortly after weaning. Each was double tagged in the interdigital webbing of the hind flippers with numbered Jumbo Rototags ® (produced by Dalton, Henley-on-Thames, UK). Tagged seals were individually identifiable by unique tag colour-number combinations.

Thorough and systematic searches of the ESA for tagged seals took place at approximately regular intervals four times a month between mid August and late November (the breeding season) and three times a month at other times of the year. This allowed for an increase in search effort during that time of the year when tag resighting was found to be more difficult. The frequency and thoroughness of the searches are thought to have detected almost all seals ashore with the probability of detecting any given female hauled out in the study area during at least one weekly resighting during any particular breeding season at 96.3% (confidence interval = 96.0-96.6% - De Bruyn *et al.* 2009). Due to their behaviour, access to seals is easer during the moult (pers. obs.) and the probability of detecting animals during this haulout should therefore be greater. Prior to May 1989 tag resights did not take place during the winter, and prior to August 1992 tag resights on the isolated south coast sections of the ESA only took place on a monthly basis. In addition to tag colour, number and location, behaviour and moult status was recorded during tag resight events. Seals were assumed to age by one year on the 15th of October of each year, unless they where hauled out in the few weeks prior to this date during the breeding season, in which case they were aged from the beginning of that breeding season.

Data editing

The mark-recapture programme generated a total of 78 218 records up to April 2004. We edited these to: (1) correct obvious errors, or remove errors where correction was not possible, (2) remove individuals of unknown sex, and (3) select a single record for each haulout event. Details of the procedures used in editing the data are recorded in Chapter 2. Following editing the database consisted of 34 082 records of 9 832 individuals

Analysis

We assessed fidelity to the natal site by seals ashore for their first reproductive haulout (RH1), fidelity to their RH1 site by seals ashore to breed a second time, and fidelity to their natal site by seals ashore to moult at age four, for males and females separately. In all cases we used two variables: (1) the duration of time since the last visit to the natal or RH1 site and (2) the number of visits to the relevant prior haulout site, before the current haulout. We examined the differences within variables by comparing the frequency distributions of categories using the Kruskal-Wallis ANOVA or the Kolmogorov-Smirnov test. Females ashore for their first reproductive haulout were restricted to animals from age three to six. Primiparity was assumed. Older apparently primiparous females were understood to have previously bred away from their natal island (though this is not necessarily true - see Oosthuizen *et al.* 2011). This was not a factor for males because of the short duration of the period during which they were adults. We chose the moult haulout at age four to assess fidelity to the natal site for two reasons. By this age sufficient time had passed to allow several visits to the natal site. Since elephant seals at the study site suffer substantial mortality, reducing the number of animals observed with each succeeding age (Pistorius *et al.* 2004; Pistorius *et al.* 2005), analysis at age four still provides a large sample size.

Results

For female elephant seals, the time elapsed since their last visit to their natal site and their first breeding haulout, has a significant effect on their fidelity to their natal site when they first breed (Kruskal-Wallis ANOVA: $H_{(4,\ 1084)} = 71.9$, $p < .001$). Where only one or two years have passed since they last hauled out at their natal site, they return within an average of less than 4.2 kilometres, whereas if more than two years have passed they return, on average, over 8.6 kilometres away (Figure 5.2a). There is no significant trend for males (Kolmogorov-Smirnov: $n_1 = 62$, $n_2 = 17$, $p > 0.01$), with all seals that had visited their natal site within the last four years breeding within 4.7 kilometres of their natal site (Figure 5.2b).

The number of past visits to the natal site between birth and the first reproductive haulout had a significant effect on fidelity to the natal site during the current haulout in both females (Kruskal-Wallis ANOVA: $H_{(2,\ 1144)} = 76.7$, $p < 0.001$) and males (Kolmogorov-Smirnov: $n_1 = 143$, $n_2 = 28$, $p < 0.025$). Females that had not visited their natal site at all hauled out on average more than twice as far from their natal site than those that had visited at least once (Figure 5.3a). For males, those that had not visited their natal site, or visited it only once, hauled out a mean distance of 7.4 kilometres from their natal site, whereas those that had visited two or three times, hauled out a mean distance of only 3.2 kilometres (Figure 5.3b).

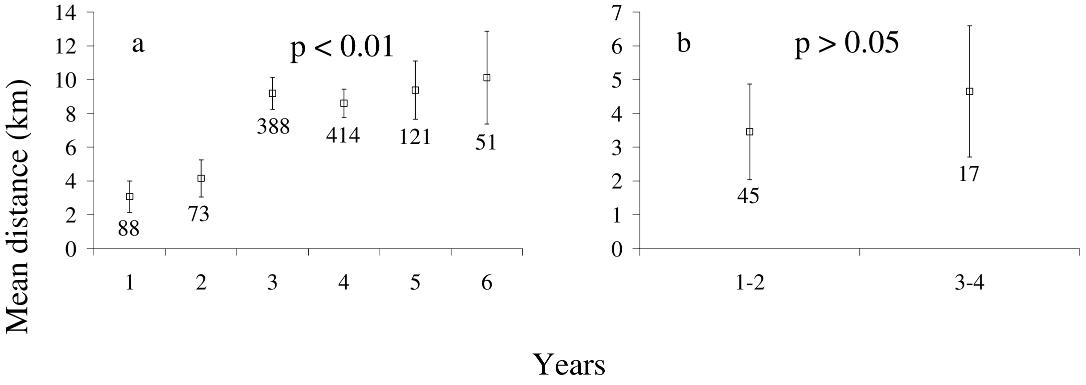


Figure 5.2 Mean distance (± 95 % confidence limits) of first breeding site from natal site and the number of years since the last visit to the natal site of southern elephant seals *Mirounga leonina* at Marion Island: (a) females and (b) males. Numbers are sample sizes.

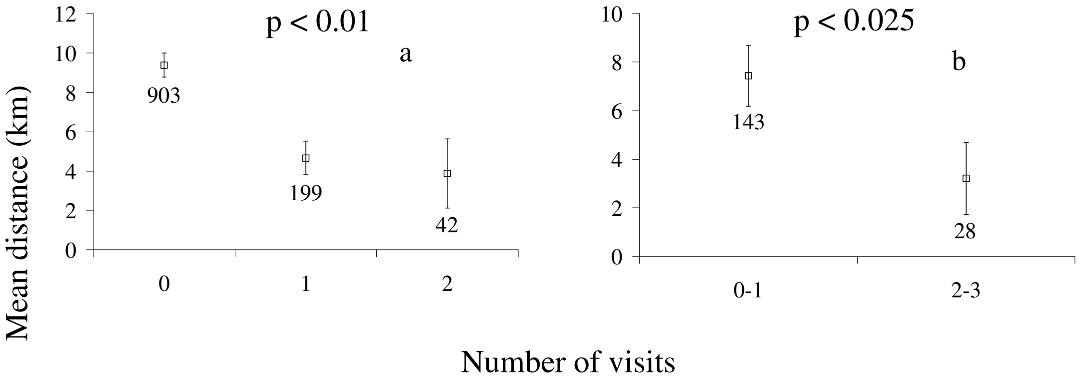


Figure 5.3 Mean distance (± 95 % confidence limits) of first breeding site from natal site and the number of visits to the natal site since birth of southern elephant seals *Mirounga leonina* at Marion Island: (a) females and (b) males. Numbers are sample sizes.

The number of years since the last visit to the RH1 site, by female elephant seals hauled out to breed a second time, had no significant influence on mean distance from the RH1 site (Kolmogorov-Smirnov: $n_1 = 546$, $n_2 = 106$, $p > 0.05$) (Figure 5.4). The sample size for males was too small to test for an effect. The number of visits by female elephant seals to the RH1 site between their primiparous and diparous haulouts was significantly associated with differences in RH1 site fidelity (Kolmogorov-Smirnov: $n_1 = 60$, $n_2 = 621$, $p < 0.005$). Females hauling out at their natal site during the intervening period were only displaced 3.6 kilometres from their RH1 site, compared to the 6.5 kilometres of those that had not visited their RH1 site (Figure 5.5a). The difference for males was not significant (Kolmogorov-Smirnov: $n_1 = 19$, $n_2 = 79$, $p > 0.05$) (Figure 5.5b).

The increase in the distance displaced between the natal site and the moult haulout visited at age four with increasing duration of time since the last visit to the natal site (Figure 5.6a and 5.6b) is not significant for both females (Kruskal-Wallis ANOVA: $H_{(3, 221)} = 3.4$, $p = 0.33$) and males (Kolmogrov-Smirnov: $n_1 = 31$, $n_2 = 13$, $p > 0.05$). When considering the number of visits, however, the difference is significant for females (Kruskal-Wallis ANOVA: $H_{(2, 757)} = 41.3$, $p < 0.001$). Females that have visited their natal site twice between birth and their moult at age four, haul out a mean distance of 4.6 kilometres from their natal site to moult at age four. Females that have not visited their natal site at all during that time period, haul out twice as far (Figure 5.7a). The difference is not significant for males (Kolmogrov-Smirnov: $n_1 = 96$, $n_2 = 29$, $p > 0.05$).

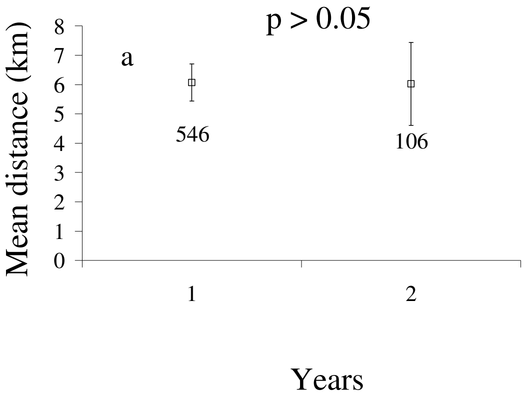


Figure 5.4 Mean distance (± 95 % confidence limits) of second breeding site from first breeding site and the number of years since the last visit to the first breeding site of female southern elephant seals *Mirounga leonina* at Marion Island. Numbers are sample sizes.

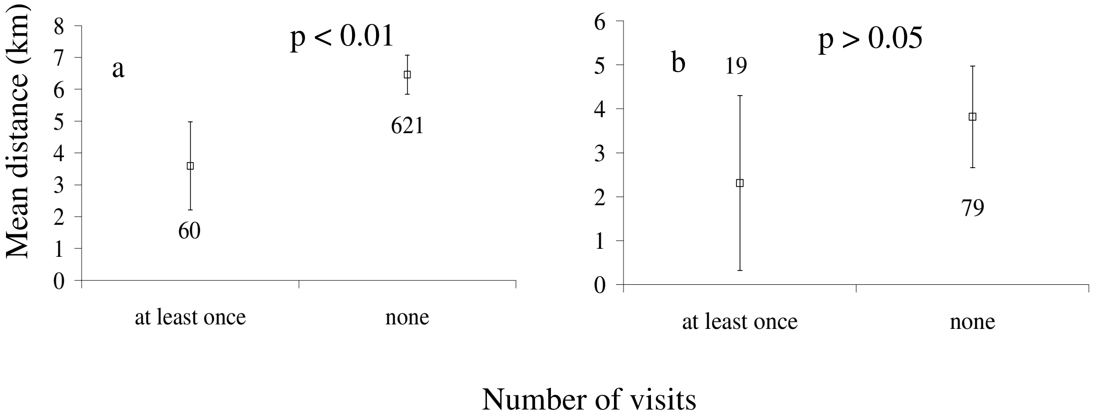


Figure 5.5 Mean distance (± 95 % confidence limits) of second breeding site from first breeding site and the number of visits to the first breeding site in the interim, of southern elephant seals *Mirounga leonina* at Marion Island: (a) females and (b) males. Numbers are sample sizes.

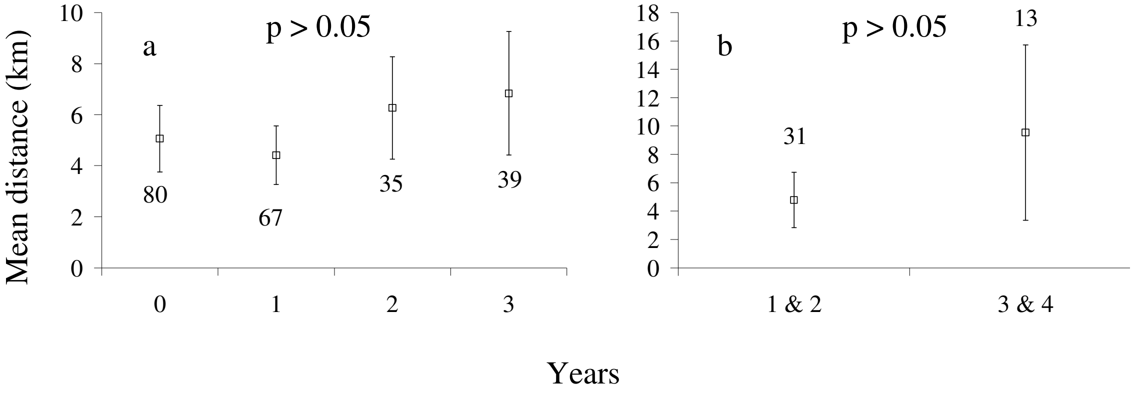


Figure 5.6 Mean distance (± 95 % confidence limits) of moult site at age four from natal site and the number of years since the last visit to the natal site of southern elephant seals *Mirounga leonina* at Marion Island: (a) females and (b) males. Numbers are sample sizes.

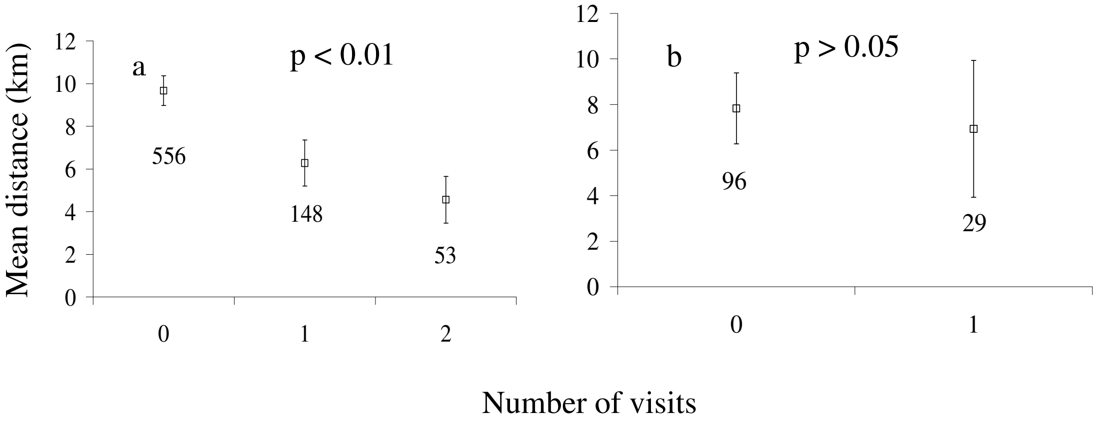


Figure 5.7 Mean distance (± 95 % confidence limits) of moult site at age four from natal site and the number of visits to the natal site in the interim of southern elephant seals *Mirounga leonina* at Marion Island: (a) females and (b) males. Numbers are sample sizes.

Discussion

In this study we assessed the effect of the passage of time on spatial memory, specifically to determine if familiarity of southern elephant seals with terrestrial haulout sites deteriorated over time. We found that a longer absence from a previously visited site and fewer visits to that site was associated with a greater distance of displacement from that site in later haulout events. Changes in site fidelity with changes in familiarity were significant for females in most cases, but generally not in males, possible because of differences in sample sizes. In females, a greater number of visits to the natal site, and a shorter duration since the last visit to the natal site were associated with greater fidelity to that site, both by seals hauling out to breed for the first time, and those hauling out to moult. While a greater number of visits to the RH1 site between the first and second breeding haulouts was associated with greater fidelity to the RH1 site during the second breeding haulout, a shorter duration since the last visit was not. The only significant association for males was between a greater number of visits to the natal site and an increased fidelity to the natal site at first breeding.

A number of studies have examined spatial memory, primarily in relation to foraging patches and food caches (Sherry *et al.* 1981; Balda & Kamil 1989; Clayton 1994; Healy & Hurley 1995; Jansen & Forget 2001; Stafford *et al.* 2006), but also in relation to site return by migratory animals (Pärt 1995; Healy *et al.* 1996; Cristol *et al.* 2003; Mettke-Hofmann & Gwinner 2003; Pravosudov *et al.* 2006). Migrants have been found to show greater spatial abilities than closely related non-migrants (Mettke-Hofmann & Gwinner 2003; Pravosudov *et al.* 2006). While these studies have noted the feats of memory, very few have considered deterioration in spatial memory over time. Shettleworth & Krebs (1982) noted that marsh tits *Parus palustris* were more likely to recover seeds that were recently cached. Jansen & Forget (2001) further noted that memory of cache locations in rodents declined over time. However, for neither of these studies was assessing deterioration in memory a specific aim.

Evidence for the deterioration of pinniped spatial memory over time comes from a number of studies. Baker (1995) noted differences in natal site fidelity in northern fur seals *Callorhinus ursinus* and that, among breeding adults, males showed less natal site fidelity than females. He attributed the lower philopatry of males to the later onset of breeding, inferring a loss of familiarity with site location over time. There are, however, alternative explanations for sex bias in dispersal (Greenwood 1980; Dobson 1982). At the study site, older primiparous female elephant seals show lower fidelity to their natal site compared to younger animals, possibly reflecting deterioration in memory. The same is true of males hauling out to breed for the first time (Hofmeyr 2000).

Our finding that a greater number of visits to the natal or first reproductive sites are associated with more accurate return to those sites points to the advantages of experience in maintaining site fidelity. In other research at the study site, we found that older multiparous seals, and those that have more breeding experience, hauled out closer to their natal site and to a previous breeding site than younger animals did (see Chapter 2). It has also been suggested that the return of immature elephant seals to the vicinity of the natal site during the winter haulout aids in maintaining familiarity to that site (Burton 1985; Pistorius & Bester 2002). In Chapter 4 we found that participation in haulouts at the natal island by immature seals was associated with greater site fidelity when they were adult.

Other evidence for the effects of prior local experience on spatial memory has been found for birds. Clayton (Clayton 1994) noted that spatial memory in marsh tits, *Parus palustris*, in terms of cache recovery, improved with experience and age. Pärt (1995) concluded that the greater philopatry of older migrant collared flycatchers *Ficedula albicollis* was due to greater prior local experience. Reed *et al.* (1998) noted that black brant *Branta bernicla nigricans* that were seen more than once in a season at their wintering site showed significantly greater winter site fidelity in subsequent years than those seen only once. In contrast, Stafford *et al*. (2006) found no improvement in spatial memory in pinyon jays *Gymnorhinus cyanocephalus* with greater experience.

Considering the evidence both that site fidelity is beneficial to migrants, and that prior recent local experience is associated with greater site fidelity (Dow & Fredga 1983; Gauthier 1990; Pärt 1990, 1991, 1994; Dauchin & Cam 2002; MacDougall-Shackleton *et al.* 2002; Pravosudov *et al.* 2006; Doligez & Pärt 2008), it is perhaps surprising that immature elephant seals do not return to the vicinity of their natal site more frequently. There are a number of explanations why this may be the case. Firstly, it is possible that the benefits of philopatry are not so great in southern elephant seals. Although they haul out closer to their natal site than expected the first time they return to breed, less than 14 % of either males or females return to that site, and less than 18 % to within one kilometre of that site (Hofmeyr 2000). There are a number of possible reasons for a lack of strict philopatry, including avoiding high levels of inbreeding, a lack of major benefits from local knowledge (that is, any one site that supports elephant seals will be suitable) and high competition among males (Hofmeyr 2000). It is also possible that immatures deliberately avoid sites favoured by breeding animals because of topographical features or the social environment (Hofmeyr 2000; Mulaudzi *et al.* 2008). During the moult, elephant seals actively search out mud wallows, whereas breeding beaches are typically flat with a pebble or sand substrate (Panagis 1984; Wilkinson 1992). During the breeding season, which partially overlaps with the moult haulout by immature animals (Kirkman *et al.* 2003; Kirkman *et al.* 2004) high levels of aggression and harassment (Galimberti *et al.* 2000c, a, b) are possible on breeding beaches. It is therefore possible that immature animals avoid breeding beaches at this time.

Finally, there are perhaps alternative explanations for a decrease in site fidelity with time. Lewis (1995) noted that, among various species of bats, site fidelity is linked to roost permanency, with species breeding in more permanent roosts showing greater fidelity. Robertson & Cooke (1999) further suggested that greater habitat stability would likely be associated with greater winter site fidelity in migratory waterfowl. Since habitats change, an animal returning to a previously visited site after a long duration of absence may be faced with unpredictable changes in habitat. The value of returning will therefore diminish for animals that begin breeding when older than their counterparts. A corollary is that the probability of habitat change will determine whether changes in site fidelity with increasing length of absence are important, which is a testable hypothesis

References

BAKER, J.D., ANTONELIS, G.A., FOWLER, C.W. & YORK, A.E. 1995. Natal site fidelity in northern fur seals, *Callorhinus ursinus*. *Animal Behaviour* **50:** 237-247.

BALDA, R.P. & KAMIL, A.C. 1989. A comparative study of cache recovery by three corvid species. *Animal Behaviour* **38:** 486-495.

BESTER, M.N. 1989. Movements of southern elephant seals and Subantarctic fur seals in relation to Marion Island. *Marine Mammal Science* **5:** 257-265.

BESTER, M.N. & PANSEGROUW, H.M. 1992. Ranging behaviour of southern elephant seal cows from Marion Island. *South African Journal of Science* **88:** 574-577.

BURTON, H.R. 1985. Tagging studies of male southern elephant seals (*Mirounga leonina* L.) in the Vestfold Hills area, Antarctica, and some aspects of their behaviour. In: *Studies of Sea Mammals in South Latitudes*, (ed) J.K. Ling & M.M. Bryden, pp. 19-30. Geographic Services (Pty) Ltd., Adelaide.

CAMPAGNA, C. & LEWIS, M. 1992. Growth and distribution of a southern elephant seal colony. *Marine Mammal Science* **8:** 387-396.

CARRICK, R., CSORDAS, S.E., INGHAM, S.E. & KEITH, K. 1962. Studies on the southern elephant seal, *Mirounga leonina* (L.). III. The annual cycle in relation to age and sex. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 119-160.

CARRICK, R. & INGHAM, S.E. 1962. Studies on the southern elephant seal, *Mirounga leonina* (L.) I. Introduction to the series. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 89-101.

CLAYTON, N.S. 1994. The role of age and experience in the behavioural development of food-storing and retrieval in marsh tits, *Parus palustris Animal Behaviour* **47:** 1435-1444.

CONDY, P.R. 1979. Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.) at Marion Island. *South African Journal of Zoology* **14:** 95-102.

CRISTOL, D.A., REYNOLDS, E.B., LECLERC, J.E., DONNER, A.H., FARABAUGH, C.S. & ZIEGENFUS, C. 2003. Migratory dark-eyed juncos, *Junco hyemalis*, have better spatial memory and denser hippocampal neurons than nonmigratory conspecifics. *Animal Behaviour* **66:** 317-328.

DAUCHIN, E. & CAM, E. 2002. Can non-breeding be a cost of breeding dispersal? *Behavioral Ecology and Sociobiology* **51:** 153-163.

DE BRUYN, P.J.N. 2009. Life history studies of the southern elephant seal population at Marion Island. Ph.D., University of Pretoria, Pretoria.

DOBSON, F.S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour* **30:** 1183-1192.

DOLIGEZ, B. & PÄRT, T. 2008. Estimating fitness consequences of dispersal: a road to 'know-where'? Non-random dispersal and the underestimation of dispersers' fitness. *Journal of Animal Ecology* **77:** 1199-1211.

DOW, H. & FREDGA, S. 1983. Breeding and natal dispersal of the Goldeneye, *Bucephala clangula*. *Journal of Animal Ecology* **52:** 681-695.

FABIANI, A., GALIMBERTI, F., SANVITO, S. & HOELZEL, A.R. 2006. Relatedness and site fidelity at the southern elephant seal, *Mirounga leonina*, breeding colony in the Falkland Islands. *Animal Behaviour* **72:** 617-626.

GALIMBERTI, F., BOITANI, L. & MARZETTI, I. 2000a. Female strategies of harassment reduction in southern elephant seals. *Ethology Ecology & Evolution* **12:** 367-388.

GALIMBERTI, F., BOITANI, L. & MARZETTI, I. 2000b. The frequency and costs of harassment in southern elephant seals. *Ethology Ecology & Evolution* **12:** 345-365.

GALIMBERTI, F., BOITANI, L. & MARZETTI, I. 2000c. Harassment during arrival on land and departure to sea in southern elephant seals. *Ethology Ecology & Evolution* **12:** 389-404.

GAUTHIER, G. 1990. Philopatry, nest-site fidelity, and reproductive performance in Buffleheads. *The Auk* **107:** 126-132.

GREENWOOD, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* **28:** 1140-1162.

HEALY, S.D., GWINNER, E. & KREBS, J.R. 1996. Hippocampal volume in migratory and non-migratory warblers: effect of age and experience. *Behavioural Brain Research* **81:** 61-68.

HEALY, S.D. & HURLEY, T.A. 1995. Spatial memory in rufous hummingbirds (*Selasphorus rufus*): A field test. *Animal Learning and Behavior* **23:** 63-68.

HINDELL, M.A. 1991. Some lif-history parameters of a declining population of southern elephant seals, *Mirounga leonina*. *Journal of Animal Ecology* **60:** 119-134.

HINDELL, M.A. & LITTLE, G.J. 1988. Longevity, fertility and philopatry of two female southern elephant seals (*Mirounga leonina*) at Macquarie Island. *Marine Mammal Science* **4:** 168-171.

HINDELL, M.A. & MCMAHON, C.R. 2000. Long distance movement of a southern elephant seal (*Mirounga leonina*) from Macquarie Island to Peter 1 ØY. *Marine Mammal Science* **16:** 504-507.

HOFMEYR, G.J.G. 2000. Dispersal and dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. M.Sc., University of Pretoria, Pretoria.

JANSEN, P.A. & FORGET, P.-M. 2001. Scatterhoarding rodents and tree regeneration. In: *Nouragues: dynamics and plant-animal interactions in a neotropical rainforest*, (ed) F. Bongers, P. Charles-Dominique, J.-M. Forget & M. Thery, pp. 275-288. Kluwer Academic Publishers, Dordrecht.

JONKER, F.C. & BESTER, M.N. 1998. Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island. *Antarctic Science* **10:** 21-30.

KIRKMAN, S.P., BESTER, M.N., HOFMEYR, G.J.G., JONKER, F.C., PISTORIUS, P.A., OWEN, R. & STRYDOM, N. 2004. Variation in the timing of the breeding haulout of female southern elephant seals at Marion Island. *Australian Journal of Zoology* **52:** 379-388.

KIRKMAN, S.P., BESTER, M.N., PISTORIUS, P.A., HOFMEYR, G.J.G., JONKER, F.C., OWEN, R. & STRYDOM, N. 2003. Variation in the timing of moult of southern elephant seals at Marion Island *South African Journal of Wildlife Research* **33:** 79-84.

LAWS, R.M. 1956. The elephant seal (*Mirounga leonina* Linn.). II. General social and reproductive behaviour. *Falkland Islands Dependencies Survey Scientific Reports* **13:** 1-88.

LAWS, R.M. 1993. Identification of species. In: *Antarctic seals: research methods and techniques*, (ed) R.M. Laws, pp. 1-28. Cambridge University Press, Cambridge.

LEWIS, S.E. 1995. Roost fidelity of bats: a review. *Journal of Mammalogy* **76:** 481-496.

LINDBERG, M.S. & SEDINGER, J.S. 1997. Ecological consequences of nest site fidelity in the black brant. *The Condor* **99:** 25-38.

MACDOUGALL-SHACKLETON, E.A., DERRYBERRY, E.P. & HAHN, T.P. 2002. Nonlocal male mountain white-crowned sparrows have lower paternity and higher parasite loads than males singing local dialect. *Behavioral Ecology* **13:** 682-689.

METTKE-HOFMANN, C. & GWINNER, E. 2003. Long-term memory for a life on the move. *Proceedings of the National Academy of Sciences* **100:** 5863-5866.

MORTON, M.L. 1992. Effects of sex and birth date on premigration biology, migration schedules, return rates and natal dispersal in the mountain white-crowned sparrow. *The Condor* **94:** 117-133.

MULAUDZI, T.W., HOFMEYR, G.J.G., BESTER, M.N., KIRKMAN, S.P., PISTORIUS, P.A., JONKER, F.C., MAKHADO, A.B., OWEN, J.H. & GRIMBEEK, R.J. 2008. Haulout site selection by southern elephant seals at Marion Island. *African Zoology* **43:** 25-33.

NICHOLS, D.G. 1970. Dispersal and dispersion in relation to the birthsite of the southern elephant seal, *Mirounga leonina* (L.), of Macquarie Island *Mammalia* **34:** 598-616.

OOSTHUIZEN, W.C., BESTER, M.N., DE BRUYN, P.J.N. & HOFMEYR, G.J.G. 2009. Intra-archipelago moult dispersion of southern elephant seals at the Prince Edward Islands, southern Indian Ocean. *African Journal of Marine Science* **31:** 457-462.

OOSTHUIZEN, W.C., BESTER, M.N., TOSH, C.A., GUINET, C., BESSON, D. & DE BRUYN, P.J.N. 2011. Dispersal and dispersion of southern elephant seals in the Kerguelen province, Southern Ocean. *Antarctic Science* **23:** 567-577.

PANAGIS, K. 1984. The influence of southern elephant seals *Mirounga leonina* (Linnaeus) on the coastal terrestrial ecology of Marion Island. M.Sc., University of Pretoria,

PARADIS, E., BAILLIE, S.R., SUTHERLAND, W.J. & GREGORY, R.D. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* **67:** 518-536.

PÄRT, T. 1990. Natal dispersal in the collared flycatcher: possible causes and reproductive consequences. *Ornis Scandinavica* **21:** 83-88.

PÄRT, T. 1991. Philopatry pays: a comparison between collared flycatcher sisters. *The American Naturalist* **138:** 790-796.

PÄRT, T. 1994. Male philopatry confers a mating advantage in the migratory collared flycatcher, *Ficedula albicollis*. *Animal Behaviour* **48:** 401-409.

PÄRT, T. 1995. Does breeding experience explain increased reproductive success with age? An experiment. *Proceedings of the Royal Society of London B* **260:** 113-117.

PISTORIUS, P.A. & BESTER, M.N. 2002. Juvenile survival and population regulation in southern elephant seals at Marion Island. *African Zoology* **37:** 35-41.

PISTORIUS, P.A., BESTER, M.N., LEWIS, M.N., TAYLOR, F.E., CAMPAGNA, C. & KIRKMAN, S.P. 2004. Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal (*Mirounga leonina*). *Journal of Zoology, London* **263:** 107-119.

PISTORIUS, P.A., BESTER, M.N. & TAYLOR, F.E. 2005. Pubescent southern elephant seal males and the food limitation hypothesis. *South African Journal of Wildlife Research* **35:** 215-218.

PISTORIUS, P.A., DE BRUYN, P.J.N. & BESTER, M.N. 2011. Population dynamics of southern elephant seals: a synthesis of three decades of demographic research at Marion Island. *South African Journal of marine Science* **33:** 523-534.

PRAVOSUDOV, V.V., KITAYSKY, A.S. & OMANSKA, A. 2006. The relationship between migratory behaviour, memory and the hippocampus: an intraspecific comparison. *Proceedings of the Royal Society of London B* **273:** 2641-2649.

REED, E.T., COOCH, E.G., GOUDIE, R.I. & COOKE, F. 1998. Site fidelity of black brant wintering and spring staging in the Strait of Georgia, British Columbia. *The Condor* **100:** 426-437.

REISINGER, R.R. & BESTER, M.N. 2010. Long distance breeding dispersal of a southern elephant seal. *Polar Biology* **33:** 1289-1291.

ROBERTSON, G.J. & COOKE, F. 1999. Winter philopatry in migratory waterfowl. *The Auk* **116:** 20-34.

ROBERTSON, R.B. 1956. *Of whales and men.* The Reprint Society, London. 255 pp.

SHERRY, D.F., KREBS, J.R. & COWIE, R.J. 1981. Memory for the location of stored food in marsh tits *Animal Behaviour* **29:** 1260-1266.

SHETTLEWORTH, S.J. & KREBS, J.R. 1982. How marsh tits find their hoards: The roles of site preference and spatial memory. *Journal of Experimental Psychology: Animal Behaviour Processes* **8:** 354-375.

STAFFORD, B.L., BALDA, R.P. & KAMIL, A.C. 2006. Does seed-caching experience affect spatial memory performance by pinyon jays? *Ethology* **112:** 1202-1208.

VAN DEN HOFF, J. 2001. Dispersal of southern elephant seals (*Mirounga leonina* L.) marked at Macquarie Island. *Wildlife Research* **28:** 413-418.

WILKINSON, I.S. 1992. Factors affecting reproductive success of southern elephant seals, *Mirounga leonina*, at Marion Island. Ph.D., University of Pretoria, Pretoria.

WINTER, Y. & STICH, K.P. 2005. Foraging in a complex naturalistic environment: capacity of spatial working memory in flower bats. *The Journal of Experimental Biology* **208:** 539-548.

Chapter 6 ▪ Conclusions

Southern elephant seal weaned pups, Marion Island. Photo – G. Hofmeyr

CHAPTER 6

CONCLUSIONS

Dispersal, site fidelity and site selection

Many studies of dispersal have been completed. These have identified a number of patterns of site selection and site fidelity by animals. Amongst these are the predominant dispersal by immature individuals, patterns of sex bias related to social systems, and differences in the dispersal of migratory and non-migratory animals (Howard 1960; Greenwood 1980; Greenwood & Harvey 1982; Shields 1987; Morton 1992; Pärt 1995). These studies have generally noted significant fidelity, during reproductive events, to natal site and first reproductive site (Greenwood 1980; Dobson 1982; Shields 1987). A number of studies have also shown fidelity by animals to sites that were inhabited during past non-reproductive events, during later events of the same type (Anderson & Sterling 1974; Herzog & Keppie 1980; Martin *et al.* 1984). To the best of my knowledge none of these studies has, however, systematically examined the dispersal of an animal over the course of its life in relation to all previous sites visited, that is, its dispersal in relation to its history of movement. This study does so, at least with regard to the terrestrial component of the life cycle of a migratory marine predator, the southern elephant seal.

The selection of a site by an animal is determined by a number of factors, including accessibility, the possibility of encountering that habitat, the availability of resources and the presence of dangers. Assessment of site suitability is also dependent on a number of factors, including an animal's knowledge of that site. This knowledge may be built up over the course of an animal's life as it explores its habitat and gains knowledge of different sites (Caughley 1977; Manley *et al.* 1993; Dingle 1996; Clobert *et al.* 2001). The animal's history of movement is therefore important in influencing the levels of dispersal and site fidelity shown. Here I examine two major aspects of dispersal, using the study animal as an example. Firstly, I describe the patterns of site fidelity of southern elephant seals in relation to their past history of movement. This is the subject of Chapters 2 and 3. I then examine the suspected influence of the seals knowledge of those sites by examining the role visits play in retaining familiarity to those sites (Chapter 4) and the possible deterioration in spatial memory over time (Chapter 5).

This study was made possible by three factors: 1. the life history of the study animal, southern elephant seals, 2. the topography of the study site, Marion Island, and 3. a long-term mark-recapture study that has allowed the terrestrial behaviour of 21 cohorts of the study animal which form part of this study, to be recorded in detail. Elephant seals are particularly suited because their life history can be divided into a number of stages, each of which can be regarded as a discrete event. That is, each stage serves a different purpose, and there is a clear separation between each stage. Being a marine migratory animal, the terrestrial phases are separated by long periods at sea during which the animal travels sufficiently far from its terrestrial habitat (Carrick *et al.* 1962b; Hindell & Little 1988; Bester & Pansegrouw 1992b; Jonker & Bester 1998) as to render the distances among various terrestrial sites at one island negligible. Furthermore, during the terrestrial component of their lives, southern elephant seals are easy to observe and their behaviour relatively easy to record. The study site has made this research possible because each site used by elephant seals is discrete. Except for one or two sites, movement among them is not possible unless the seals return to sea. In addition, these sites are relatively easy for observers to access within a short period, allowing all seals ashore to be recorded during one unit of time, and to access with sufficient frequency to provide the resolution necessary for this study. The population at the study site is also small enough to allow all animals to be marked within weeks of birth. Finally, the mark-recapture programme at the study site has generated data concerning the behaviour of elephant seals of sufficient resolution to follow aspects of their terrestrial behaviour relevant to this study. This research programme is probably unique.

Site fidelity and history of movement

Past research on elephant seals indicates that they preferentially select specific sites based on their sex and age group, and the particular type of haulout for which they come ashore (Mulaudzi *et al.* 2008). A number of authors have suggested that these sites are possibly selected because of their topography (Nichols 1970; Panagis 1985; Mulaudzi *et al.* 2008; Setsaas *et al.* 2008), or because of social factors (Galimberti *et al.* 2000a, b; Hofmeyr 2000; Pistorius *et al.* 2002a; Mulaudzi *et al.* 2008). Elephant seals have further been shown to select sites based on their past experience of particular sites, that is, to display significant fidelity to particular terrestrial sites, or areas. This includes fidelity to their natal sites and past reproductive haulout sites, both at Marion Island (Panagis 1981; Wilkinson & Bester 1990; Hofmeyr 2000) and elsewhere (Nichols 1970; Huber *et al.* 1991; Lewis *et al.* 1996; Fabiani *et al.* 2006), and site fidelity during non-breeding haulouts (Lenglart & Bester 1982; Hofmeyr 2000; Setsaas *et al.* 2008). This study indicates that southern elephant seals at Marion Island show significantly greater fidelity to a number of sites visited during the course of their lives, other than their natal and breeding sites. It also indicates that the patterns of fidelity shown change over the course of their lives.

Immature female southern elephant seals haul out significantly closer to their previous haulout site than to their natal site. This pattern is evident whether they are hauling out for the winter or to moult. When they return to breed for the first time, however, they haul out closer to the natal site than to any other site. Despite this, the natal site is not significantly closer than sites visited in the previous year. Conversely, when they return to breed they haul out closest to their previous breeding site, and significantly closer to this site than to other sites, including their natal site, except for a number of recently visited haulout sites. Moulting adult females return closest to their previous moult haulout. Therefore adult females haul out closest to the site of their previous haulout event of the same type as the current event.

It is possible that the fidelity shown during the winter and moult to sites other than their natal site is because habitat requirements during these types of haulouts are different to those of reproductive haulouts. For the moult haulout, at least, elephant seals preferentially use mud wallows, which are unlike the flat pebble or sand beaches occupied during reproductive haulouts (Laws 1956; Carrick *et al.* 1962b; Mulaudzi *et al.* 2008; Setsaas *et al.* 2008). Fidelity to the natal site is expected during reproductive haulout events since the animal’s own survival is proof of the suitability of this site for reproduction (Boulinier & Danchin 1997; Switzer 1997). However, while female elephant seals tend to return to the vicinity of their natal site to reproduce, they show greater fidelity to haulout sites used for previous reproductive events. It is possible that the temporal hiatus between birth and reproduction has lead to a loss of familiarity with the birth site. This is supported by the finding that older diparous and multiparous females breed farther from their natal site than younger animals.

Differences in site fidelity between males and females

In view of the great differences in morphology (Bininda-Emonds & Gittleman 2000; Lindenfors *et al.* 2002) and life history (Payne 1977; Lander 1981; Warneke & Shaughnessy 1985; Trillmich 1987; Laws 1993; Butterworth *et al.* 1995) shown by pinnipeds in general, and elephant seals in particular (Laws 1956; Carrick & Ingham 1962; Condy 1979; Laws 1993; Kirkman *et al.* 2003; Kirkman *et al.* 2004; McIntyre *et al.* 2010), differences in patterns of behaviour, including dispersal, are expected. Previous research at the study site has shown that this is so. Hofmeyr (2000) proposed that the greater natal and first reproductive site fidelity shown by breeding adult males at Marion Island was possibly due to their greater mobility at this time (adult females cannot move far because of their dependent and relatively immobile pups), and indeed Munyai (2006) showed that this was the case. This study shows further differences in dispersal between the sexes.

Immature male elephant seals at the study site haul out closest to the sites of their previous haulout events. This pattern continues when they first haul out to breed. Although they haul out significantly closer to their natal site than would be expected by chance during this event (Hofmeyr 2000), they haul out significantly closer to the sites of recent haulout events. Subsequently as adults, they come ashore closest to the site of the previous haulout event of the same type, that is, they moult closest to the site of their previous moult haulout and breed closest to the site of their previous reproductive haulout. Thus the difference between males and females in the patterns of dispersal shown over the course of their lives is fidelity to the natal site during the first reproductive event. It is possible that the later onset of maturity in males is relevant. The duration of the period between birth and first reproduction is more than twice as long in males as in females (McCann 1980). Their decline in spatial memory may therefore be correspondingly greater.

It is, however, possible that other factors play a role. As noted, males have a greater ability to move among sites and may therefore have more opportunity to assess the value of a site, especially in relation to social factors. The quantity of adult females (as a reproductive resource) and the quality of adult males (as competitors) may play a role. While reproductive success may not be as site dependent in adult females, social factors may also be important. Adult females are subject to considerable harassment during the breeding season (Galimberti *et al.* 2000c, b) which may lead them to select specific sites (Mulaudzi *et al.* 2008) or pursue alternative mating strategies (de Bruyn *et al.* 2011). However, high levels of harassment do not appear to result in physical injuries to females, or to reduce adult females' success at raising pups to weaning age (Galimberti *et al.* 2000b). While the impact of site selection in terms of the social environment may be relatively unimportant for females, in a polygynous species these may have major consequences in terms of reproductive success of males.

Familiarity with a site and the winter haulout

Chapters 2 and 3 indicate that familiarity with a site may be important in determining the level of fidelity to that site. I further examined the relevance of site familiarity by assessing the role of the winter haulout undertaken by immature seals in Chapter 4.

Elephant seals come ashore for four types of terrestrial periods. While the purpose of the natal period, the moult haulout and the reproductive haulout are known, the winter haulout serves no obvious purpose (Carrick *et al.* 1962a, b). In view of the obvious costs associated with moving to a terrestrial haulout site in terms of time and energy expenditure (Hindell & Burton 1988; Bester & Pansegrouw 1992a; Wilkinson 1992; Jonker & Bester 1998), fasting (Slip et al. 1992) and predation (Condy *et al.* 1978; Ridoux 1986; Guinet 1991; Keith *et al.* 2001; Pistorius *et al.* 2002b; Tosh *et al.* 2008), the winter haulout must have associated benefits and a number have been suggested (Burton 1985), including maintaining familiarity with the natal environment (Pistorius *et al.* 2002a).

This study found that greater participation in the winter haulout by females was associated with greater natal site fidelity during first reproductive haulout. This was not the case for multiparous females, which is not surprising in view of their greater fidelity to their previous breeding site than to their natal site. This seems to support the suggestion that the winter haulout serves to maintain site familiarity. However, a return by immature female elephant seals to moult at the natal island is also associated with greater natal site fidelity when hauling to breed as an adult. In fact, greater fidelity by adults is associated with any haulout by those animals at the natal island when immature, irrespective of whether it is during the winter or to moult. If the moult haulout then also serves to maintain familiarity with a site, is the winter haulout really necessary? It is possible that it does augment the winter haulout in maintaining site familiarity, but this study does not confirm that it is the purpose of the winter haulout. A critical assessment of the other suggested reasons for the winter haulout indicates that many are not feasible. However, the possibilities that this period serves to allow for the strengthening of dentine in an animal that dives continuously while at sea, or as training and conditioning for terrestrial activities, have yet to be assessed.

Forgetful elephant seals

The role played by familiarity with a terrestrial haulout site was further assessed in Chapter 5 by examining the possibility of a decline in spatial memory over time. A number of studies have suggested that spatial memory may deteriorate over time (Balda & Kamil 1989; Morton 1992; Winter & Stich 2005) possibly leading to a decrease in site fidelity in migratory animals. This is important since returning to a previously used site has been shown to have benefits in terms of finding suitable habitat, obtaining resources, avoiding dangers, and finding a mate (Pärt 1990, 1991; Morton 1992; Pärt 1995; Paradis *et al.* 1998; Robertson & Cooke 1999; Dauchin & Cam 2002; Doligez & Pärt 2008).

At Marion Island both natal site fidelity and first reproductive site fidelity of female southern elephant seals is linked to two factors: the duration of absence since the last visit to that site, and the number of visits to that site. This is true for both the moult and the reproductive haulout. While the same is possibly true of males, smaller sample sizes prevent a conclusion from being drawn. These results indicate the advantages of prior recent local experience in maintaining site fidelity. This possibly explains the patterns shown in Chapters 2 and 3. These indicate that, while elephant seals haul out closer to their natal site than expected, they haul out even closer, and significantly so, to recently visited sites in all but one instance. The exception is the great fidelity primiparous females show to their natal site.

There are, however, alternative explanations for a perceived decline in site fidelity with longer duration of absence and fewer visits. Since habitats may change, a longer duration of absence may be associated with a greater possibility of change to that habitat, and therefore a greater possibility that it is no longer the most suitable.

A synthesis

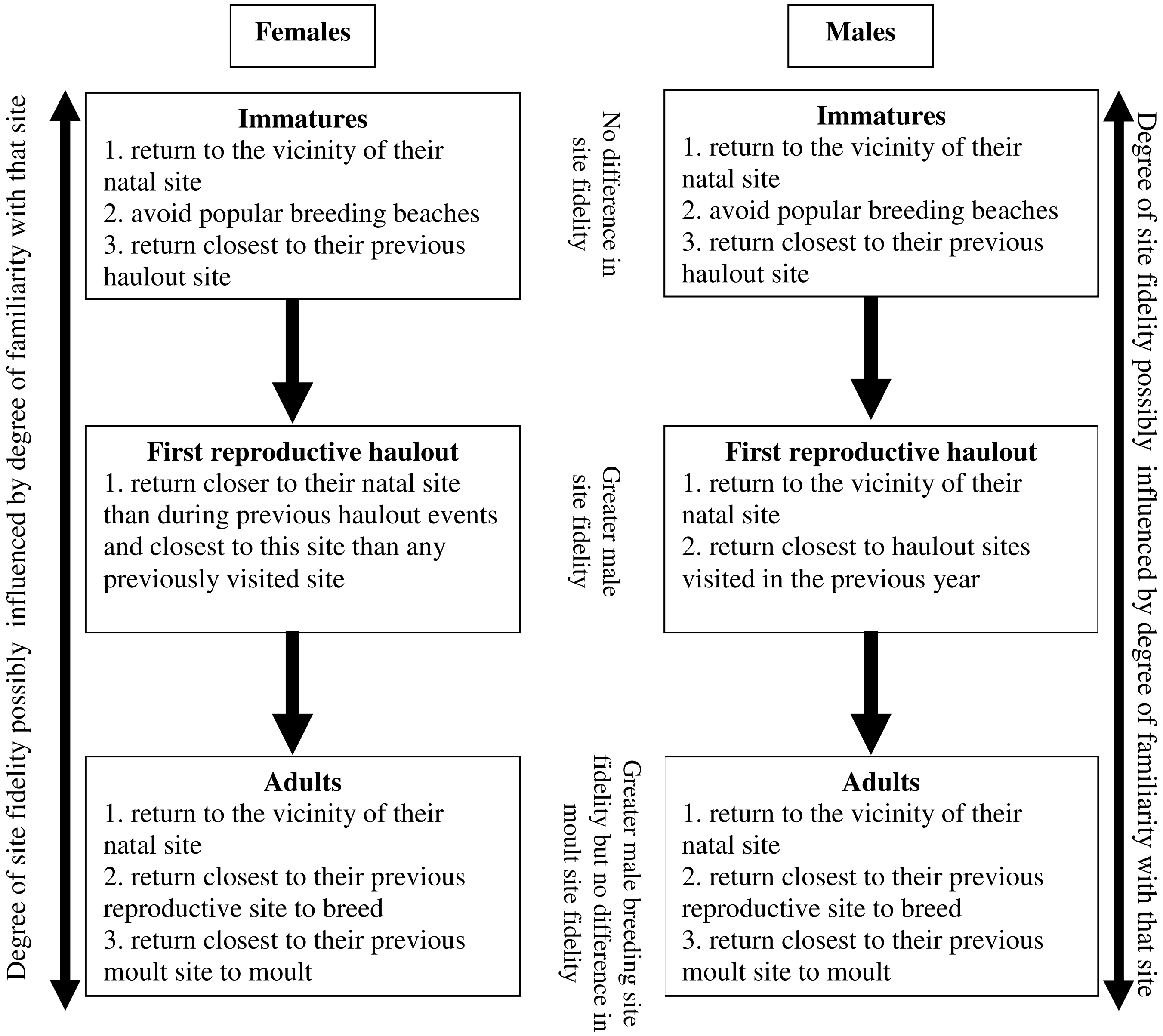


Figure 6.1 Schematic diagram showing lifetime changes in the patterns of dispersal by male and female southern elephant seals *Mirounga leonina* at Marion Island.

Further avenues for research

This study is necessarily limited and gives a partial picture of the site fidelity of southern elephant seals at the study site over the course of their lives. Further complimentary research is required to remedy this.

1. This study notes the role of history of movement as a determinant of site selection. Other factors may be important in terms of why an animal chooses or happens to inhabit the location that it does at any one time. Therefore one needs to compare history of movement to the roles played by current information obtained about a site by the animal, in terms of physical environment, but also in terms of the social environment.
2. The past history of the animal in terms of reproductive success may be an important influence on dispersal. For example, do smaller females tend to disperse farther and more often, and larger disperse less? Will females that have lost a pup prior to weaning disperse farther? Are adult males more likely to return to sites where they have been beachmasters, but less likely to return to sites where they have been bachelors?
3. What role does ability to move play in dispersal? As mentioned above, males and females differ in mobility and further research to examine the consequences of this is required. Important work has been done on the fine scale movements of grey seals when ashore and shown how these can be related to characteristics of their terrestrial environment (Pomeroy *et al.* 2000; Twiss *et al.* 2000; Redman *et al.* 2001; Twiss *et al.* 2002). Similar work is possible on southern elephant seals at the study site.
4. Also important is influence of other haulout sites. As noted, research has shown that seals move between Marion and neighbouring Prince Edward Island and

between the Marion and islands that lie farther away (Bester 1989; Oosthuizen *et al.* 2009; Oosthuizen *et al.* 2011). If possible, higher levels of tag resight efforts at these sites are required.

5. Many studies of dispersal use a site fidelity index, that is, a measure of strict philopatry (for example Baker *et al.* 1995). This study examines dispersal by comparing the frequency distributions of distances animals are displaced from sites used during a previous haulout event. A comparison of these methods using the same database would possibly result in a complementary picture but may also indicate which method is more suitable.
6. An age-related bias is possible since the characteristics of dispersal were assumed to be unrelated to the duration of an animal's life span. It is possible that animals surviving for more years than the average behaved differently than those that did not. While these animals only form a portion of the group of younger animals they comprise the entire group for older animals. A comparison of the dispersal of long-term and short term survivors is therefore required.

References

ANDERSON, D.R. & STERLING, R.T. 1974. Population dynamics of molting pintail drakes banded in south-central Saskatchewan. *Journal of Wildlife Management* **38:** 266-274.

BAKER, J.D., ANTONELIS, G.A., FOWLER, C.W. & YORK, A.E. 1995. Natal site fidelity in northern fur seals, *Callorhinus ursinus*. *Animal Behaviour* **50:** 237-247.

BALDA, R.P. & KAMIL, A.C. 1989. A comparative study of cache recovery by three corvid species. *Animal Behaviour* **38:** 486-495.

BESTER, M.N. 1989. Movements of southern elephant seals and Subantarctic fur seals in relation to Marion Island. *Marine Mammal Science* **5:** 257-265.

BESTER, M.N. & PANSEGROUW, H.M. 1992a. Ranging behaviour of southern elephant seal cows from Marion Island. *South African Journal of Science* **88:** 574-575.

BESTER, M.N. & PANSEGROUW, H.M. 1992b. Ranging behaviour of southern elephant seal cows from Marion Island. *South African Journal of Science* **88:** 574-577.

BININDA-EMONDS, O.R.P. & GITTLEMAN, J.L. 2000. Are pinnipeds functionally different from fissiped carnivores? The importance of phylogenetic comparative analyses. *Evolution* **54:** 1011-1023.

BOULINIER, T. & DANCHIN, E. 1997. The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. *Evolutionary Ecology* **11:** 505-517.

BURTON, H.R. 1985. Tagging studies of male southern elephant seals (*Mirounga leonina* L.) in the Vestfold Hills area, Antarctica, and some aspects of their behaviour. In: *Studies of Sea Mammals in South Latitudes*, (ed) J.K. Ling & M.M. Bryden, pp. 19-30. Geographic Services (Pty) Ltd., Adelaide.

BUTTERWORTH, D.S., PUNT, A.E., OOSTHUIZEN, W.H. & WICKENS, P.A. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 3. Modelling the dynamics of the Cape fur seal *Arctocephalus pusillus pusillus*. *South African Journal of Marine Science* **16:** 161-183.

CARRICK, R., CSORDAS, S.E., INGHAM, S.E. & KEITH, K. 1962a. Studies of the southern elephant seal, *Mirounga leonina* (L.). III. The annual cycle in relation to age and sex. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 119-160.

CARRICK, R., CSORDAS, S.E., INGHAM, S.E. & KEITH, K. 1962b. Studies on the southern elephant seal, *Mirounga leonina* (L.). III. The annual cycle in relation to age and sex. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 119-160.

CARRICK, R. & INGHAM, S.E. 1962. Studies on the southern elephant seal, *Mirounga leonina* (L.) I. Introduction to the series. *Commonwealth Science and Industrial Research Organisations, Wildlife Research* **7:** 89-101.

CAUGHLEY, G. 1977. *The analysis of vertebrate populations.* John Wiley, Chichester. 234 pp.

CLOBERT, J., DANCHIN, E., DHONDT, A. & NICHOLS, J.D. 2001. *Dispersal.* Oxford University Press, Oxford. 452 pp.

CONDY, P.R. 1979. Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.) at Marion Island. *South African Journal of Zoology* **14:** 95-102.

CONDY, P.R., VAN AARDE, R.J. & BESTER, M.N. 1978. The seasonal occurence and behaviour of killer whales Orcinus orca, at Marion Island. *Journal of Zoology, London* **184:** 449-464.

DAUCHIN, E. & CAM, E. 2002. Can non-breeding be a cost of breeding dispersal? *Behavioral Ecology and Sociobiology* **51:** 153-163.

DE BRUYN, P.J.N., TOSH, C.A., BESTER, M.N., CAMERON, E.Z., MCINTYRE, T. & WILKINSON, I.S. 2011. Sex at sea: alternative mating system in an extremely polygynous mammal. *Animal Behaviour* **82:** 445-451.

DINGLE, H. 1996. *Migration: the biology of life on the move.* Oxford University Press, Oxford. 474 pp.

DOBSON, F.S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour* **30:** 1183-1192.

DOLIGEZ, B. & PÄRT, T. 2008. Estimating fitness consequences of dispersal: a road to 'know-where'? Non-random dispersal and the underestimation of dispersers' fitness. *Journal of Animal Ecology* **77:** 1199-1211.

FABIANI, A., GALIMBERTI, F., SANVITO, S. & HOELZEL, A.R. 2006. Relatedness and site fidelity at the southern elephant seal, *Mirounga leonina*, breeding colony in the Falkland Islands. *Animal Behaviour* **72:** 617-626.

GALIMBERTI, F., BOITANI, L. & MARZETTI, I. 2000a. Female strategies of harassment reduction in southern elephant seals. *Ethology Ecology & Evolution* **12:** 367-388.

GALIMBERTI, F., BOITANI, L. & MARZETTI, I. 2000b. The frequency and costs of harassment in southern elephant seals. *Ethology Ecology & Evolution* **12:** 345-365.

GALIMBERTI, F., BOITANI, L. & MARZETTI, I. 2000c. Harassment during arrival on land and departure to sea in southern elephant seals. *Ethology Ecology & Evolution* **12:** 389-404.

GREENWOOD, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* **28:** 1140-1162.

GREENWOOD, P.J. & HARVEY, P.H. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* **13:** 1-21.

GUINET, C. 1991. L'orque (*Orcinus orca*) authour de l'archipel Crozet comparaison avec d'autres localites. *Revue de Ecologie (Terre at la Vie)* **46:** 321-337.

HERZOG, P.W. & KEPPIE, D.M. 1980. Migration in a local population of spruce grouse. *The Condor* **82:** 366-372.

HINDELL, M.A. & BURTON, H.R. 1988. The history of the elephant seal industry at Macquarie Island and an estimate of the pre-sealing numbers. *Papers and Proceedings of the Royal Society of Tasmania* **122:** 159-168.

HINDELL, M.A. & LITTLE, G.J. 1988. Longevity, fertility and philopatry of two female southern elephant seals (*Mirounga leonina*) at Macquarie Island. *Marine Mammal Science* **4:** 168-171.

HOFMEYR, G.J.G. 2000. Dispersal and dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. M.Sc., University of Pretoria, Pretoria.

HOWARD, W.E. 1960. Innate and environmental dispersal of individual vertebrates. *American Midland Naturalist* **63:** 152-161.

HUBER, H.R., ROVETTA, A.C., FRY, L.A. & JOHNSTON, S. 1991. Age-specific natality of northern elephant seals at the South Farallon Islands, California. *Journal of Mammalogy* **72:** 525-534.

JONKER, F.C. & BESTER, M.N. 1998. Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island. *Antarctic Science* **10:** 21-30.

KEITH, M., BESTER, M.N., BARTLETT, P.A. & BAKER, D. 2001. Killer whales (Orcinus orca) at Marion Island, Southern Ocean. *African Zoology* **36:** 163-175.

KIRKMAN, S.P., BESTER, M.N., HOFMEYR, G.J.G., JONKER, F.C., PISTORIUS, P.A., OWEN, R. & STRYDOM, N. 2004. Variation in the timing of the breeding haulout of female southern elephant seals at Marion Island. *Australian Journal of Zoology* **52:** 379-388.

KIRKMAN, S.P., BESTER, M.N., PISTORIUS, P.A., HOFMEYR, G.J.G., JONKER, F.C., OWEN, R. & STRYDOM, N. 2003. Variation in the timing of moult of southern elephant seals at Marion Island *South African Journal of Wildlife Research* **33:** 79-84.

LANDER, R.H. 1981. A life table and biomass estimate for Alaskan fur seals. *Fisheries Research* **1:** 55-70.

LAWS, R.M. 1956. The elephant seal (*Mirounga leonina* Linn.). II. General social and reproductive behaviour. *Falkland Islands Dependencies Survey Scientific Reports* **13:** 1-88.

LAWS, R.M. 1993. Identification of species. In: *Antarctic seals: research methods and techniques*, (ed) R.M. Laws, pp. 1-28. Cambridge University Press, Cambridge.

LENGLART, P.Y. & BESTER, M.N. 1982. Post-weaning dispersion of southern elephant seal *Mirounga leonina* underyearlings at Kerguelen. *Revue d'Écologie (Terre et la Vie)* **36:** 175-186.

LEWIS, M., CAMPAGNA, C. & QUINTANA, F. 1996. Site fidelity and dispersion of southern elephant seals from Patagonia. *Marine Mammal Science* **12:** 138-147.

LINDENFORS, P., TULLBERG, B.S. & BIUW, M. 2002. Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behavioral Ecology and Sociobiology* **52:** 188-193.

MANLEY, B., MCDONALD, L. & THOMAS, D. 1993. *Resource selection by animals. Statistical design and analysis for field studies.* Chapman and Hall, London. 221 pp.

MARTIN, A.R., KATONA, S.K., MATILLA, D., HEMBREE, D. & WATERS, T.D. 1984. Migration of humpback whales between the Caribbean and Iceland. *Journal of Mammalogy* **65:** 330-333.

MCCANN, T.S. 1980. Population structure and social organization of southern elephant seals, *Mirounga leonina* (L.). *Biological Journal of the Linnean Society* **14:** 133-150.

MCINTYRE, T., DE BRUYN, P.J.N., ANSORGE, I.J., BESTER, M.N., BORNEMANN, H., PLÖTZ, J. & TOSH, C.A. 2010. A lifetime at depth: vertical distribution of southern elephant seals in the water column. *Polar Biology* **33:** 1037-1048.

MORTON, M.L. 1992. Effects of sex and birth date on premigration biology, migration schedules, return rates and natal dispersal in the mountain white-crowned sparrow. *The Condor* **94:** 117-133.

MULAUDZI, T.W., HOFMEYR, G.J.G., BESTER, M.N., KIRKMAN, S.P., PISTORIUS, P.A., JONKER, F.C., MAKHADO, A.B., OWEN, J.H. & GRIMBEEK, R.J. 2008. Haulout site selection by southern elephant seals at Marion Island. *African Zoology* **43:** 25-33.

MUNYAI, F.M. 2006. Intersite movement by southern elephant seals ashore at Marion Island. M.Sc., University of Pretoria, Pretoria.

NICHOLS, D.G. 1970. Dispersal and dispersion in relation to the birthsite of the southern elephant seal, *Mirounga leonina* (L.), of Macquarie Island *Mammalia* **34:** 598-616.

OOSTHUIZEN, W.C., BESTER, M.N., DE BRUYN, P.J.N. & HOFMEYR, G.J.G. 2009. Intra-archipelago moult dispersion of southern elephant seals at the Prince Edward Islands, southern Indian Ocean. *African Journal of Marine Science* **31:** 457-462.

OOSTHUIZEN, W.C., BESTER, M.N., TOSH, C.A., GUINET, C., BESSON, D. & DE BRUYN, P.J.N. 2011. Dispersal and dispersion of southern elephant seals in the Kerguelen province, Southern Ocean. *Antarctic Science* **23:** 567-577.

PANAGIS, K. 1981. Local movement of southern elephant seal pups *Mirounga leonina* (Linn.) at Marion Island. *South African Journal of Antarctic Research* **10/11:** 28-31.

PANAGIS, K. 1985. The influence of elephant seals on the terrestrial ecosystem at Marion Island. In: *Antarctic Nutrient cycles and Food Webs*, (ed) W.R. Siegfried, P.R. Condy & R.M. Laws, pp. 173-179. Springer-Verlag,

PARADIS, E., BAILLIE, S.R., SUTHERLAND, W.J. & GREGORY, R.D. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* **67:** 518-536.

PÄRT, T. 1990. Natal dispersal in the collared flycatcher: possible causes and reproductive consequences. *Ornis Scandinavica* **21:** 83-88.

PÄRT, T. 1991. Philopatry pays: a comparison between collared flycatcher sisters. *The American Naturalist* **138:** 790-796.

PÄRT, T. 1995. Does breeding experience explain increased reproductive success with age? An experiment. *Proceedings of the Royal Society of London B* **260:** 113-117.

PAYNE, M.R. 1977. Growth of a fur seal population. *Philosophical Transactions of the Royal Society, London, B* **279:** 67-79.

PISTORIUS, P.A., KIRKMAN, S.P., BESTER, M.N. & TAYLOR, F.E. 2002a. Implications of the winter haulout for future survival and resighting probablity of southern elephant seals at Marion Island. *South African Journal of Wildlife Research* **32:** 59-63.

PISTORIUS, P.A., TAYLOR, F.E., LOUW, C., HANISE, B., BESTER, M.N., DE WET, C., DU PLOOY, A., GREEN, N., KLASEN, N., PODILE, S. & SCHOEMAN, J. 2002b. Distribution, movement, and estimated population size of killer whales at Marion Island, December 2000. *South African Journal of Wildlife Research* **32:** 1-7.

POMEROY, P.P., TWISS, S.D. & REDMAN, P. 2000. Philopatry, site fidelity and local kin associations within grey seal breeding colonies. *Ethology* **106:** 899-919.

REDMAN, P., POMEROY, P.P. & TWISS, S.D. 2001. Grey seal maternal attendance patterns are affected by water availability on North Rona, Scotland. *Canadian Journal of Zoology* **79:** 1073-1079.

RIDOUX, V. 1986. Feeding association between seabirds and killer whales, *Orcinus orca*, around subantarctic Crozet Islands. *Canadian Journal of Zoology* **65:** 2113-2115.

ROBERTSON, G.J. & COOKE, F. 1999. Winter philopatry in migratory waterfowl. *The Auk* **116:** 20-34.

SETSAAS, T.H., BESTER, M.N., VAN NIEKERK, J.H., ROUX, J.-P. & HOFMEYR, G.J.G. 2008. Dispersion during the moult haulout of southern elephant seals at the Courbet Peninsula, Iles Kerguelen. *Polar Biology* **31:** 249-253.

SHIELDS, W.M. 1987. Dispersal and mating systems: investigating their causal connections. In: *Mammalian dispersal patterns: the effects of social structure on population genetics*, (ed) B.D. Chepko-Sade & Z.T. Halpin, pp. 3-24. University of Chicago Press, Chicago.

SLIP, D.J., GALES, N.J. & BURTON, H.R. 1992. Body-mass loss, utilization of blubber and fat, and energetic requirements of male southern elephant seals, *Mirounga leonina*, during the molting fast. *Australian Journal of Zoology* **40:** 235-243.

SWITZER, P.V. 1997. Past reproductive success affects future habitat selection. *Behavioral Ecology and Sociobiology* **40:** 307-312.

TOSH, C.A., DE BRUYN, P.J.N. & BESTER, M.N. 2008. Preliminary analysis of the social structure of killer whales, *Orcinus orca*, at subantarctic Marion Island. *Marine Mammal Science* **24:** 929-940.

TRILLMICH, F. 1987. Galapagos fur seal, *Arctocephalus galapagoensis*. In: *Status, biology and ecology of fur seals. Proceedings of an international symposium and workshop, Cambridge, England, 23–27 April 1984.* , (ed) J.P. Croxall & R.L. Gentry, pp. NOAA Technical report NMFS **51:** 23-28,

TWISS, S.D., CAUDRON, A., POMEROY, P.P., THOMAS, C.J. & MILLS, J.P. 2000. Finescale topographical correlates of behavioural investment in offspring by female grey seals, *Halichoerus grypus*. *Animal Behaviour* **59:** 327-338.

TWISS, S.D., WRIGHT, N.C., DUNSTONE, N., REDMAN, P., MOSS, S. & POMEROY, P.P. 2002. Behavioral evidence of thermal stress from overheating in U. K. breeding gray seals. *Marine Mammal Science* **18:** 455-468.

WARNEKE, R.M. & SHAUGHNESSY, P. 1985. *Arctocephalus pusillus*, the South African and Australian fur seal: Taxonomy, evolution, biogeography, and life history. In: *Studies of sea mammals in south latitudes*, (ed) J.K. Ling & M.M. Bryden, pp. 53-77. South Australia Museum, Adelaide.

WILKINSON, I.S. 1992. Factors affecting reproductive success of southern elephant seals, *Mirounga leonina*, at Marion Island. Ph.D., University of Pretoria, Pretoria.

WILKINSON, I.S. & BESTER, M.N. 1990. Duration of post-weaning fast and local dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. *Journal of Zoology, London* **222:** 591-600.

WINTER, Y. & STICH, K.P. 2005. Foraging in a complex naturalistic environment: capacity of spatial working memory in flower bats. *The Journal of Experimental Biology* **208:** 539-548.

SUMMARY

Introduction

1. Studies of dispersal in animals have identified a number of common patterns related to age and sex class, social system and migratory status. These studies have noted significant fidelity to natal site and to the site of the first reproductive event. Few have considered fidelity to other sites, and none have done so systematically for all site used by an animal during the course of its life.
2. This study attempts to remedy this by examining the dispersal and site fidelity of a migratory marine predator, the southern elephant seal, in relation to its history of terrestrial site use. The patterns of site use over the course of the seals' lives and differences between males and females were examined.
3. This study also attempts to assess the role played by haulouts of immature animals in later site fidelity, and thereby assess whether the winter haulout serves to maintain site fidelity. The study further examines the deterioration in spatial memory over time.

Methods

4. The study was made possible by the life history of the southern elephant seals, by the topography of the study site, Marion Island, and by a long-term mark-recapture programme in place at the study site that has resulted in the tagging of almost all elephant seals born at the study site since 1983, and the recording of individual terrestrial behaviour at high resolution.

Results

5. Previous studies have shown that elephant seals at the study site haul out significantly closer to their natal site than expected by chance. However, this study shows that they haul out even closer to a number of other sites previously used.
6. Female immature elephant seals haul out significantly closer to the site of a previous haulout than to their natal haulout, irrespective of whether the current haulout is during the winter or to moult. Returning for their first breeding event, they haul out closest to their natal site than to all other sites, but not significantly so to a number of recent haulout sites. As adults, females haul out closest to the site of the prior haulout of the same type, that is, moulting close to or at the site of the previous moult site and breeding close to or at the site of the previous reproductive haulout.
7. While the pattern shown by primiparous females did not differ much amongst older and younger animals, older animals did haul out closer to their previous haulout site than to their natal site, though not significantly so. Older diparous and multiparous females bred significantly closer to their previous haulout site than to their natal site. There was no significant difference in the distance displaced between these sites for younger females
8. While the pattern of dispersal shown by male and female elephant seals is generally similar, there are important differences. Young immature males haul out closest to their previous haulout site but no closer to this site than to their natal site or several other sites. Older immature animals, however, haulout out significantly closer to the sites of recent haulouts only.

9. Hauling out for their first terrestrial breeding event, males come ashore significantly closest to the site of their previous haulout than other sites, including the natal site. Returning as adults, male elephant seals haul out closest to the site of their previous haulout of the same type.
10. Primiparous females showed greater natal site fidelity if they had been recorded ashore as immatures during the winter haulout. However, recorded presence as an immature during the moult haulout was also associated with greater site fidelity.
11. In female elephant seals, an increase in the duration of the period of absence from a site, and a lower number of visits to a site, were associated lower fidelity to that site. The same pattern was evident for males, although it was not significant, possibly due to the small sample size available for analysis.

Discussion

12. The lack of strict fidelity to the natal site is possibly due to a number of factors, including those related to the benefits derived from site familiarity, social factors, anthropogenic disturbance, topographical influences, and deterioration in spatial memory over time. Only some of these were examined in this thesis.
13. Differences in site requirements of different types of haulouts may lead to seals that haul out to moult or during the winter, selecting other sites in preference to their natal site.
14. Immature seals may also avoid sites popular with breeding adults to evade conspecific harassment.
15. Public information may also be important, especially for adult males during the breeding season. They have an opportunity to move among sites since they are

not hampered by the presence of a dependant and immobile pup, as females are shortly after the onset of their breeding season haulout. Males may base site selection decisions on factors such as the quantity of adult females present (a breeding resource) and the quality of adult males (potential competitors).

16. While the purpose of the winter haulout by immature seals may be to maintain familiarity with the natal site, ensuring greater familiarity when seals return as adults, recorded participation in moult haulouts by immatures is also associated with greater natal site fidelity later in life. While this thesis provides support for this theory concerning the winter haulout, the reason for its existence remains unknown. Although many of the suggested reasons for this haulout are untenable, some are possible and need to be tested.
17. This study indicates the advantages of familiarity with a site in terms of site fidelity. There are, however, possible alternative explanations for the reduced site fidelity associated with reduced experience of a site.
18. This study is subject to a number of assumptions and limitations, and also suggests a number of directions for future research.

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. Referred to as the winter haulout in this thesis.
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	Displacement from the first reproductive site and subsequent reproductive sites.
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	Displacement of an animal from its natal site, or site of reproduction, to another site where reproduction (mating or parturition) takes place.
Foraging trip	Period of time spent at sea between haulout events and assumed to be of at least 30 days duration.
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 move among sites, and therefore, be recorded at several sites.
History of movement	The record of the interseasonal movements of that animal that result in a pattern of displacements among seasonally used sites over the course of that animal's life. It does not refer to finer scale movements of animals on a day-to-day basis, or even within a season period.
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 replace their old pelage and outer layer of skin. The moulting season typically extends from early November to late April.
Natal dispersal	Displacement from the natal site to the first site of attempted reproduction.
Natal site	The site at which an animal is born.
Philopatry	The tendency for an animal to stay in, or return to, its natal site.

Post weaning haulout	Period spent ashore by weaned pups prior to their first extended pelagic phase. Technically speaking, not a haulout since these animals have yet to go to sea for an extended period.
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 to the onset of their first extended foraging trip.
Site	Portion of coastline at which seals can haul out. All but two sites are separated from others by coastal cliffs impassable to elephant seals making them natural geographical units.
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.
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 sixth birthday.
Underyearling	Age class of seals in their first year, but which have left land for their first extended foraging trip.
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. Also known as the autumn-winter haulout.
Yearling	Age class of seals in their second year.

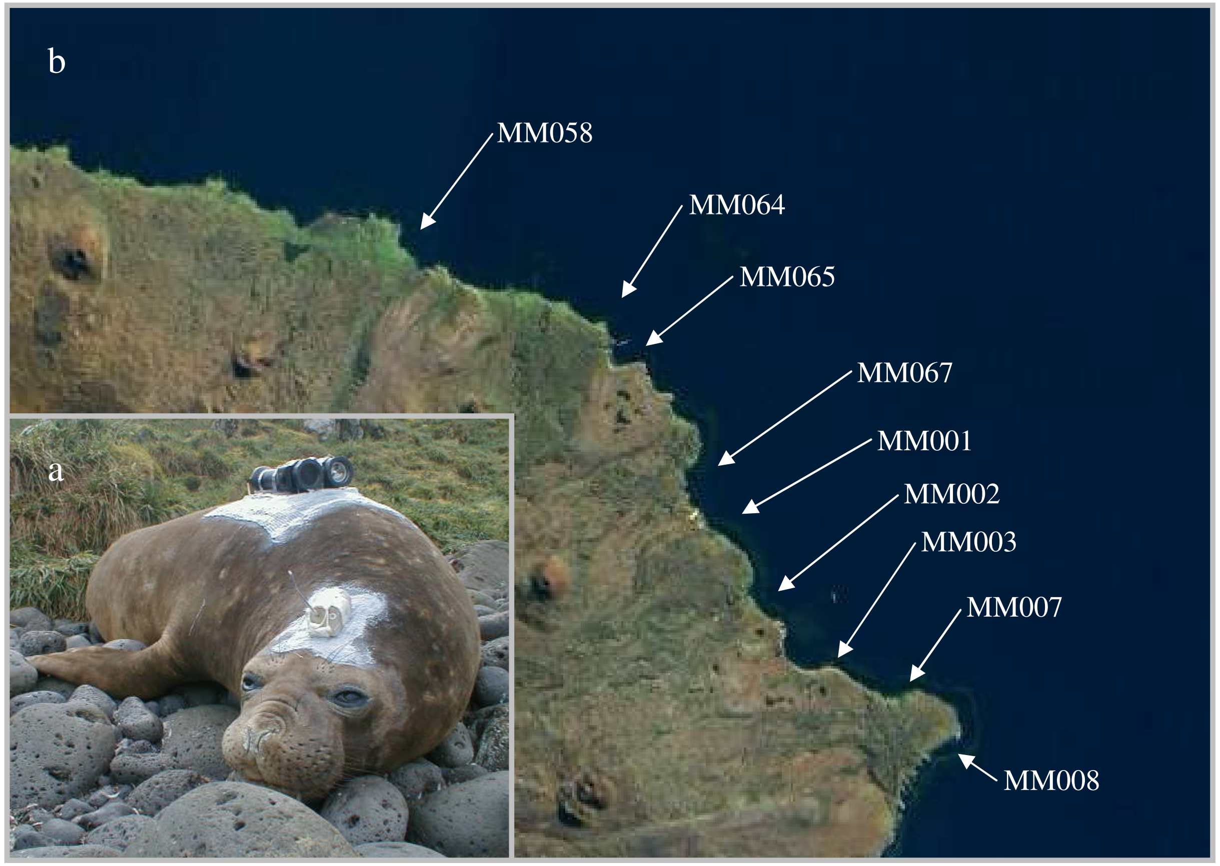
APPENDIX 2 INDIVIDUAL DATA RECORD – FEMALE WITH TAG WHITE BLACK 052 (WB052)

Table A2 Haulout records of the southern elephant seal with the tag WB052

Age	Haulout type	Site	Distance from natal site
0	Natal	MM002	0
0	Winter	MM003	1.225
1	Moult	MM008	4.75
1	Winter	MM007	3.05
2	Moult	MM067	2.71
3	Moult	MM064	6.065
3	Winter	MM001	1.275
4	Moult	MM058	9.14
5	Breeding	MM001	1.275
5	Moult	MM007	3.05
6	Breeding	MM007	3.05
6	Moult	MM007	3.05
7	Moult	MM007	3.05
8	Breeding	MM007	3.05
8	Moult	MM065	5.065
9	Breeding	MM002	0

Figure A2a Female elephant seal with tag WB052 at Trypot Beach (MM002) at the age of nine. She has been fitted with a satellite tag and a still-picture data logger. Photo G Hofmeyr.

Figure A2b Locations of haulouts on Marion Island by WB052.



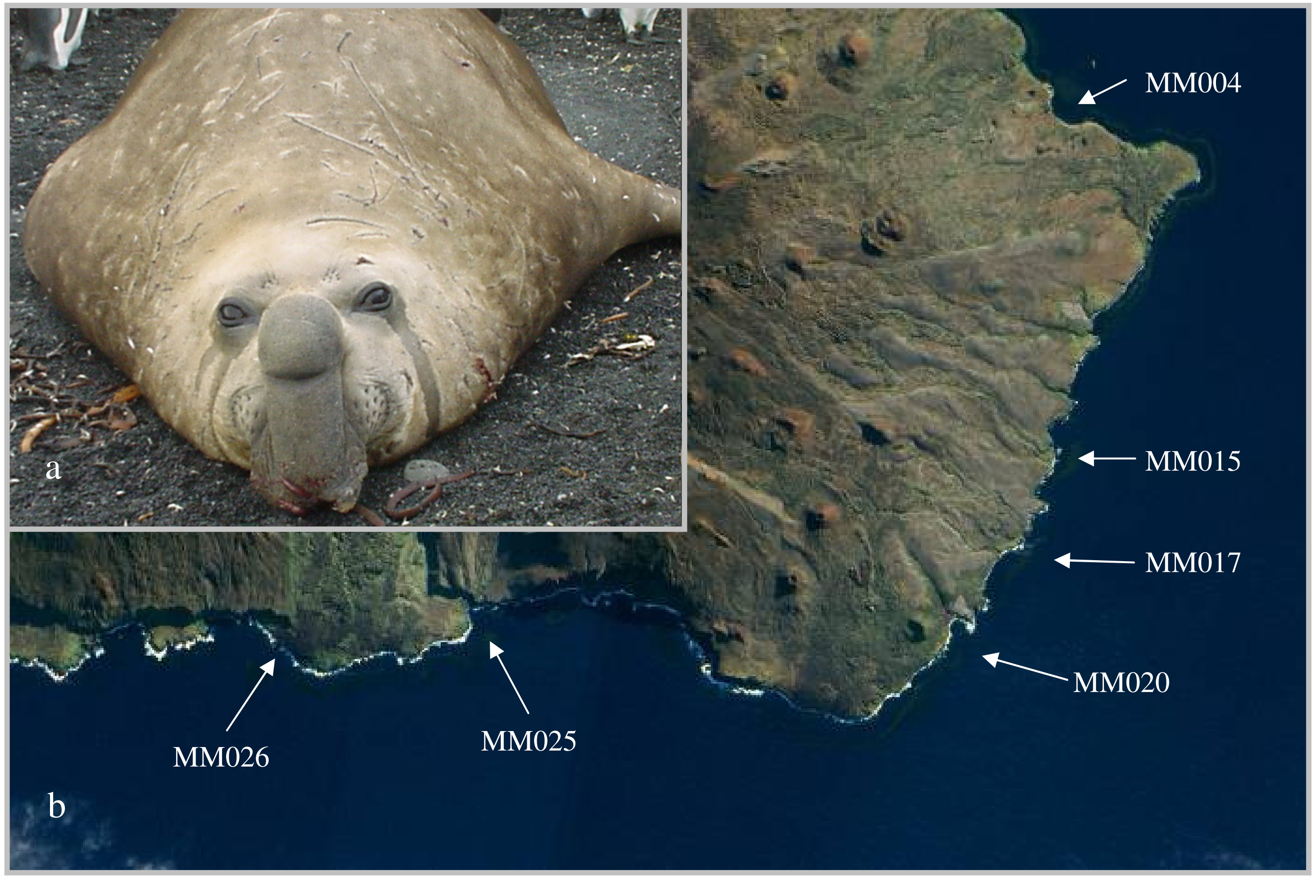
APPENDIX 3 INDIVIDUAL DATA RECORD – MALE WITH TAG ORANGE BLUE 478 (OB478)

Table A2 Haulout records of the southern elephant seal with the tag OB478

Age	Haulout type	Site	Distance from natal site
0	Natal	MM026	0
0	Winter	MM017	17.925
1	Moult	MM004	29.1
1	Winter	MM015	19.575
2	Moult	MM026	0
2	Winter	MM025	5.125
3	Moult	MM025	5.125
3	Winter	MM020	15.45
4	Moult	MM026	0
5	Moult	MM026	0
5	Winter	MM025	5.125
6	Moult	MM026	0
7	Moult	MM025	5.125
8	Breeding	MM025	5.125
9	Breeding	MM026	0
9	Moult	MM025	5.125
10	Breeding	MM026	0
10	Moult	MM025	5.125
11	Breeding	MM026	15.45
12	Breeding	MM026	0
12	Moult	MM025	5.125

Figure A3a Male elephant seal with tag OB478 at Good Hope Bay (MM026) at the age of twelve. Photo PJN de Bruyn.

Figure A3b Locations of haulouts on Marion Island by OB478.



APPENDIX 4 HAULOUT SITES ON MARION ISLAND

Table A4 Southern elephant seal haulout sites at Marion Island. Entries in bold type are classified as major parturition sites.

Code	Site	Distance to nearest (other) major parturition site (km)
MM001	Boulder Beach	1.3
MM002	**Trypot Beach**	**1.6**
MM003	Macaroni Bay, North	0.4
MM004	**Macaroni Bay, South**	**1.5**
MM005	Macaroni Bay, Rocks	0.1
MM006	**Archway Bay**	**0.2**
MM007	Archway Beach	1.5
MM008	East Cape	1.3
MM009	Hansen Cove	1.9
MM010	Tiny Beach	-
MM011	**Bullard Bay, North**	**0.3**
MM012	**Bullard Bay, South**	**0.3**
MM013	Killer Whale Cove	1.4
MM014	Waterfall Beach	0.3
MM015	**Landfall Beach**	**0.8**
MM016	**Sealer’s Cave**	**0.8**
MM017	Whale Bird Point	1.0
MM018	**Funk Bay**	**1.0**
MM019	Kildalkey Rocks	0.5
MM020	**Kildalkey Bay**	**1.0**
MM021	Hooker Cove	-

Table A4 (continued)

Code	Beach	Distance to nearest (other) major parturition site (km)
MM022	Cape Hooker	-
MM023	Puisie Beach	-
MM024	Crawford Bay	-
MM025	Watertunnel Beach	5.1
MM026	Goodhope Bay, East	5.1
MM027	Goodhope Bay, West	0.8
MM028	Rooks Peninsula	-
MM029	Rooks Bay, East	-
MM030	Rooks Bay, West	-
MM031	Vrystaat Point	-
MM032	Cape Crozier	-
MM033	La Grange Kop	12.0
MM034	Swarkop Point	16.3
MM035	Swartkop – Kaalkoppie	-
MM036	Kaalkoppie Beach	-
MM037	Kaalkoppie – Sickle Cove	-
MM038	Sickle Cove	-
MM039	Sickle Cove – Fur Seal Bay	-
MM040	Fur Bay Bay	-
MM041	Fur Seal Peninsula	-
MM042	Mixed Pickle Cove	-
MM043	Mixed Pickle Cove – Triegaardt Bay	-
MM044	Triegaardt Bay	-
MM045	Triegaardt Bay – Cape Davis	-

Table A4 (concluded)

Code	Site	Distance to nearest (other) major parturition site (km)
MM046	Cape Davis, Sealer's Beach	8.3
MM047	Cape Davis, Cliff Beach	-
MM048	Cape Davis, Steep Beach	-
MM049	Lou-se-Kop	-
MM050	Boot Rock Cove	-
MM051	Storm Petrel Bay	2.6
MM052	Storm Petrel B. - Goney Bay	1.3
MM053	**Goney Bay**	**2.2**
MM054	Goney Bay – Log Beach	0.6
MM055	Log Beach	0.7
MM056	**King Penguin Bay**	**1.6**
MM057	King Penguin Bay – Pinnacle Beach	0.6
MM058	**Pinnacle Beach**	**0.9**
MM059	Sea Elephant Bay	0.2
MM060	**Blue Petrel Bay**	**0.9**
MM061	Blue Petrel Bay – Sealer's Beaches	-
MM062	**Sealer's Beaches**	**1.0**
MM063	Sealer's South	0.3
MM064	Sealers South – Ship's Cove	1.0
MM065	**Ship's Cove**	**2.3**
MM066	Duiker's Point	1.6
MM067	Rockhopper Bay	2.4
MM068	Van den Boogaard Beach	1.7

APPENDIX 5 LIST OF HAULOUT EVENTS

Figure A5 Recorded haulout events of 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, where more than one is recorded per year. Numbers in parentheses indicate the number of seals tagged on Marion Island recorded hauling out for each haulout event from November 1983 to November 2003.

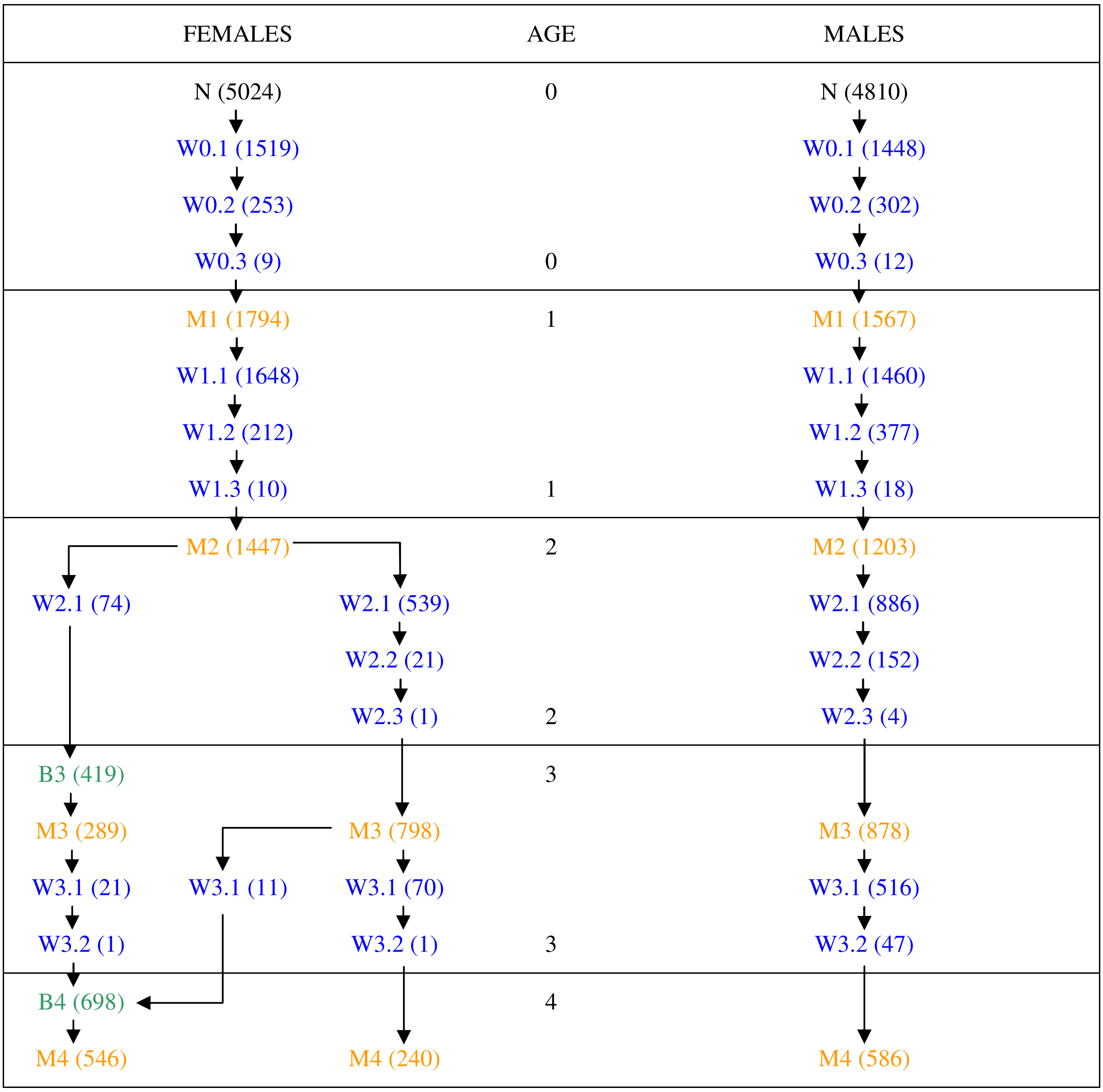


Figure A5 (continued)

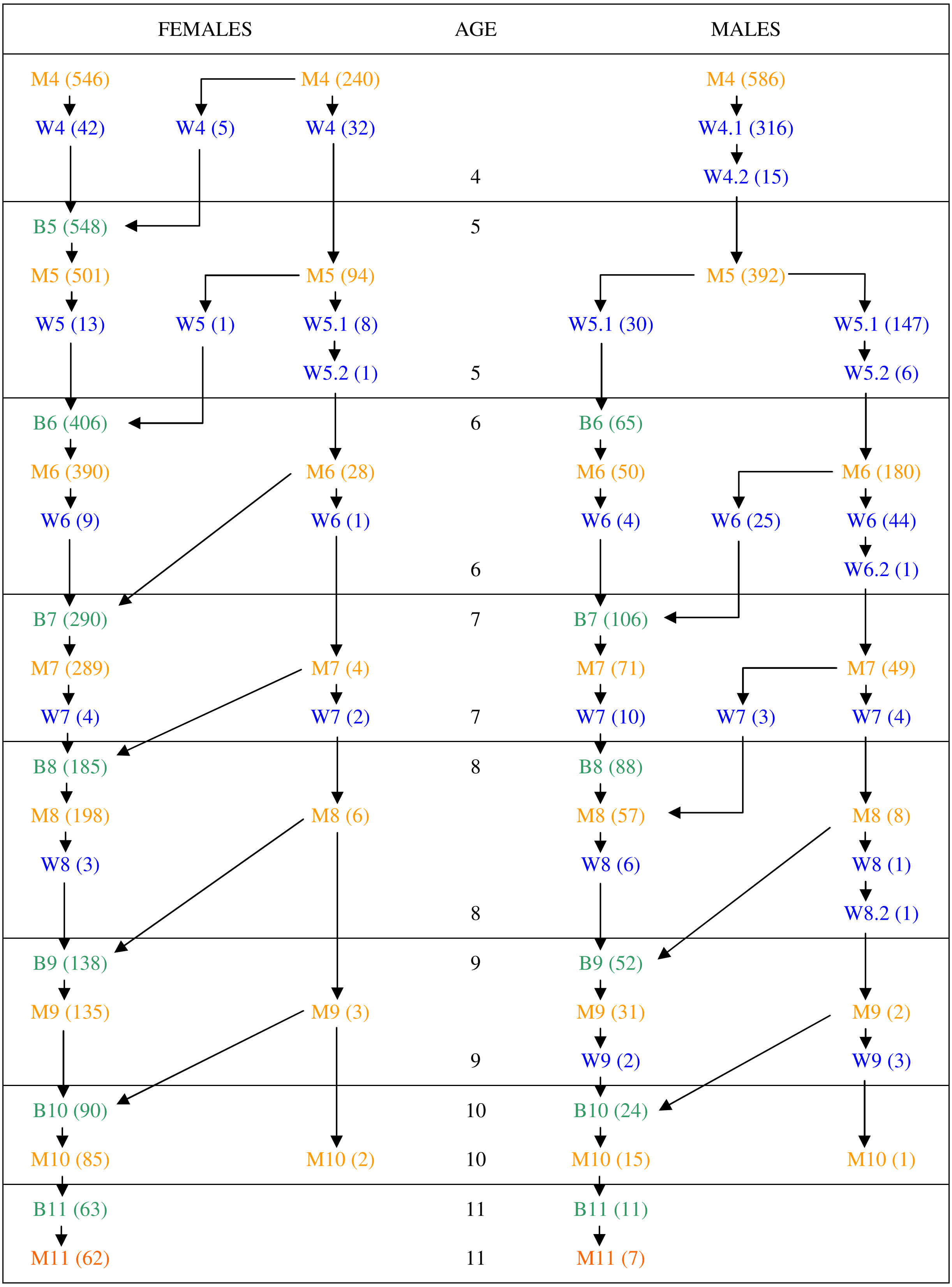


Figure A5 (concluded)

FEMALES	AGE	MALES
M11 (62)	11	M11 (7)
B12 (50)	12	B12 (5)
M12 (41)	12	M12 (2)
B13 (21)	13	B13 (1)
M13 (16)	13	M13 (2)
B14 (12)	14	B14 (1)
M14 (13)	14	M14 (1)
B15 (7)	15	
M15 (6)	15	
B16 (4)	16	
M16 (5)	16	
B17 (3)	17	
M17 (2)	17	
M18 (1)	18	

APPENDIX 6 "A SEA LYON OF JUAN FERNÁNDEZ"

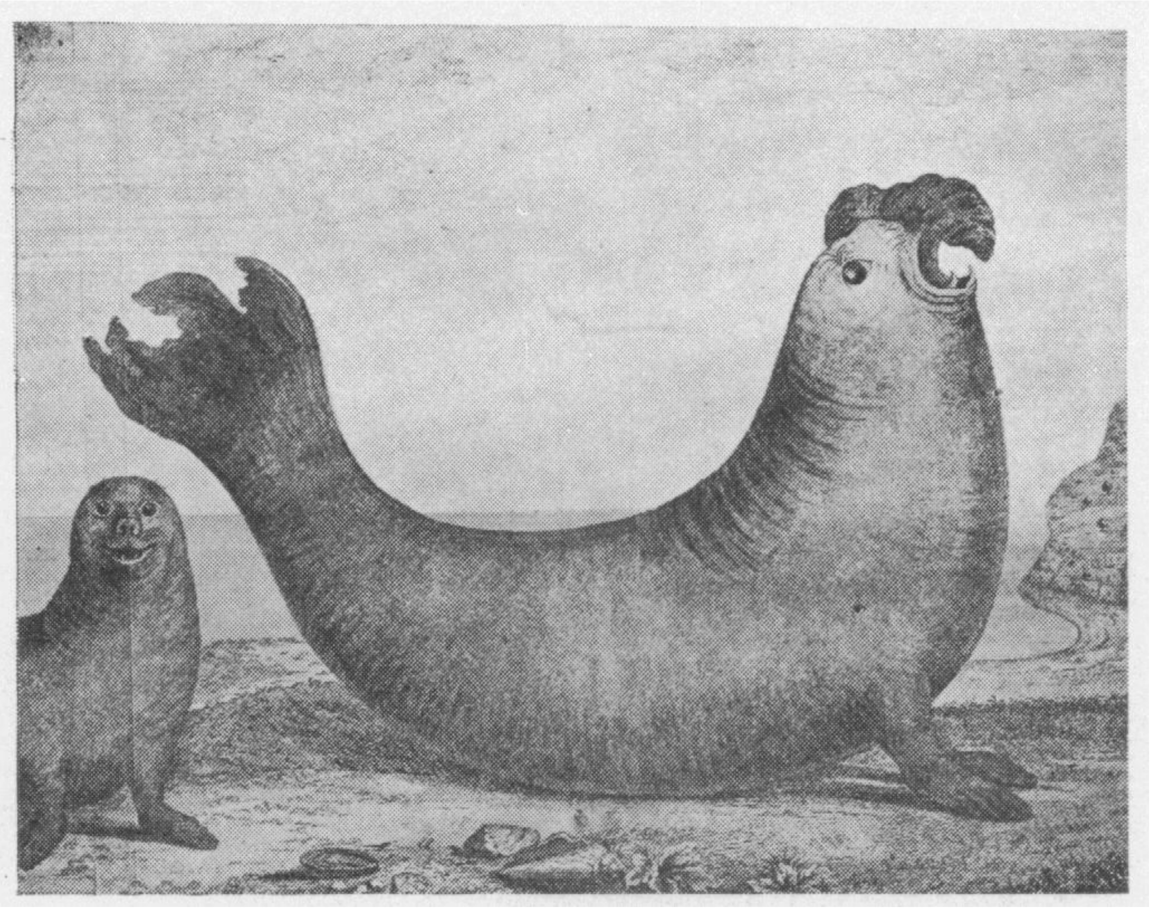


Figure A6 "A Sea Lyon of Juan Fernandez."

The above engraving and following description are from Walter (1748). Richard Walter was the chaplain who accompanied Commodore (later lord) George Anson on his brave and dangerous circumnavigation of the world from 1740 to 1744. Only one of eight ships and 188 of 1900 men completed this voyage of discovery. Five ships and some 1400 men were lost; the rest having turned back before Cape Horn. The badly provisioned expedition was subject to storms, shipwreck, mutinies, clashes with indigenous people, disease and starvation but the survivors returned with fabulous wealth, having captured a Spanish treasure galleon near the Philippines. During the voyage the expedition made landfall at the uninhabited and relatively unknown Juan Fernández Islands where they encountered the now extinct population of southern elephant seals. These they use as a source of food and cruel entertainment (Walter 1748). Walter's description and figure of the "Sea Lyons", and specimens collected during the trip, were used by Carl von Linné when assigning the binomial *Phoca leonina* in 1758. Cuvier reassigned the species to *Macrorhinus leonina* in 1824 and finally Gray named it *Mirounga leonina* in 1827 (Laws 1954). While the name employed by Walters, "Sea Lyon" or Sea Lion", is confusing because of modern usage to describe a number of species of pinnipeds of the Family Otariidae, his description and figure are clearly of the animal known today as an elephant seal and is remarkably accurate.

Page 226:

"Here we found abundance of Goats, Dogs, Sea Lions, Seals, Bream, Cod, and Crawfish as big as a middling lobster…."

Page 227:

"The Sea Lions we kill'd chiefly for Harflets, which eat as fine as any Calfs Pluck in the World; sometimes indeed we used to cut their Flesh into Stakes and broil it; it eats somewhat like Beef-steak, and is of the same colour when dress'd. The reason why they are so call'd as we imagine, is from their roaring, which is very much like that of land Lions, and in their Heads also much resembling them, they have four large Teeth before, the rest thick, short and stubbed; their hind Parts are very different; they are very large, some of them being near twice the Bigness of a Horse; they have four Fins; the two foremost, which are about half a Yard long, serve them, when ashore, to stump along, drawing the hinder Part after them, the two hindermost being only of use to them in the Water; they have short Hair of a light Colour, but lighter when young than old, for when old they look more sandy; their Prey is all in the Water, their Food being Fish, but being of an amphibious Kind, they generally come upon the Land to sleep; five or six frequently come and huddle together like Swine, and lie so for two or three Days, if not molested; they are very fat, and produce considerable Quantity of Oil, some of which we used in our Lamps, and also in frying our Fish, it having no unpleasant Taste. They are much afraid of a Man, for as soon as they see him, or apprehend they are in Danger from any thing near them, they immediately make to the Water, (for they never venture very far from it.) Some of our People would frequently get on the Backs and ride them. If they are close pursued, they will frequently turn about and raise their Body up with the Fore-fins, and face the Pursuer, standing with their Mouths wide open upon their Guard. One of our People was unfortunately torn to Pieces by them. Our method of killing them when we wanted them to eat, or their Oil, was to clap a Pistol just to their Mouths as they stand open, and so fire it down their Throats; but when we had Mind to have some Diversion with them, which we call'd *Lion bating*, then each of us took a Half pike in his Hand, and so prick'd them to Death, which commonly was sport for three or four hours before we kill'd them, and oftentimes they would find us work enough; but they being heavy unwieldy Creatures, and we assaulting them before and behind, and all round, generally conquer'd them in the end, yet they often would put us a little to the Scower; and sometimes the Creature would run himself, but knew not which way; for we commonly go between the Water and him. We kill'd one which was almost twenty-four foot long, fifteen round and seventeen Inches deep in Fat."

References

COUSTEAU, J.-Y. & DIOLÉ, P. (1974) *Sea lion, elephant seal, walrus.* Cassell, London. 304 pp.

LAWS, R.M. 1954. The elephant seal (*Mirouga leonina* Linn.). I. Growth and age. *Falkland Islands Dependencies Survey Scientific Reports* **8:** 1-62.

WALTER, R. 1748. *A Voyage to the South Seas, and to many other Parts of the World, Performed from September 1740, to June 1744, by Commodore Anson In his Majesty's Ship the Centurion, having under his Command the Goucester, Pearl, Severn, Wager, Trial, and two Store Ships.* R. Walker, London. 462 pp.

"…and we discovered that he is a passionate admirer of the elephant seal."

Jacque-Yves Cousteau & Philippe Diolé (1974)