

INTERSITE MOVEMENT BY SOUTHERN ELEPHANT SEALS ASHORE AT MARION  
ISLAND

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## ABSTRACT

Data from an on-going mark resight program at Marion Island from November 1983 to April 2004 was used to investigate the patterns and frequency of intersite movements of southern elephant seals (*Mirounga leonina*) during haulout events. The number of times each seal moved, the number of sites visited and the distance covered were used to determine the patterns and frequency of intersite movement by males and females of different age classes during natal, winter, moult and breeding haulouts. The interactions between age class and sex, and between haulout type and sex were significant for all three measures of movement. Southern elephant seals show substantial differences in the patterns of movement between males and females. While there is an increase with age in the number of times moved, the number of sites visited and the distance moved by males, this is not the case for females. Adult males on average moved significantly more often (> 4 times) than adult females, and male elephant seals in general moved significantly more than females during both the moult and the breeding haulouts. In general, adult males visited on average significantly more sites (1.64) than adult females (1.18). This was the result of different obligations of the two sexes during the different haulouts. Subadult and adult males on average moved significantly further than their female counterparts, and males moved significantly further than females during the moult (m= 1.81 km, f= 1.59 km) and breeding (3 times more) haulout.

Age has no influence on the patterns of intersite movement by breeding females for all three measures. For breeding males, however, age has a significant influence in number of times an animal moved and the distance it moved. Older mature breeding males (9 & 10+ year-olds) moved more frequently and further than younger breeders (6 & 7-year-olds) because mature animals were often involved in dominance interactions in defence of their harems or access to cows. Breeding males differ significantly from breeding females of all comparable ages: they moved significantly more often, visited more sites and moved further than breeding females. This is because females need to be with dependent and relatively immobile pups for most of the duration of the breeding season. While moulting males and females showed no clear pattern of behaviour in all three measures of intersite movement, age did have a significant influence. Amongst males, 6 and 7-year-olds moved significantly more often and visited significantly more sites than 1 to 5-year-olds and 1 to 4-year-olds, respectively. Amongst moulting females, immature animals (1 & 2-year-olds) moved significantly more often, visited more sites and moved further than mature animals. This was possibly a result of the different obligations of these groups prior to the moult haulout where adult females were involved in the strenuous and energy taxing breeding haulout. During the moult

of males and females of comparable ages, males older than 1 year moved significantly more than females of the same ages. In addition, moulting males between 1 and 8 years of age visited significantly more sites than females of the same ages and moulting males between 2 and 8 years old moved further than moulting females of similar ages. Although age has no significant influence in all three measures of movements within both wintering males and females, a significant difference is found when comparing corresponding ages of the two sexes, with males being more adventurous than females in terms of all three measures of movements. This was likely a result of earlier maturity in females, as participation level in the winter haulout at Marion Island declines before individual's haulout to breed or become pregnant

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## CHAPTER 1

### GENERAL INTRODUCTION

#### 1.1 Southern Elephant Seals

##### 1.1.1 Description

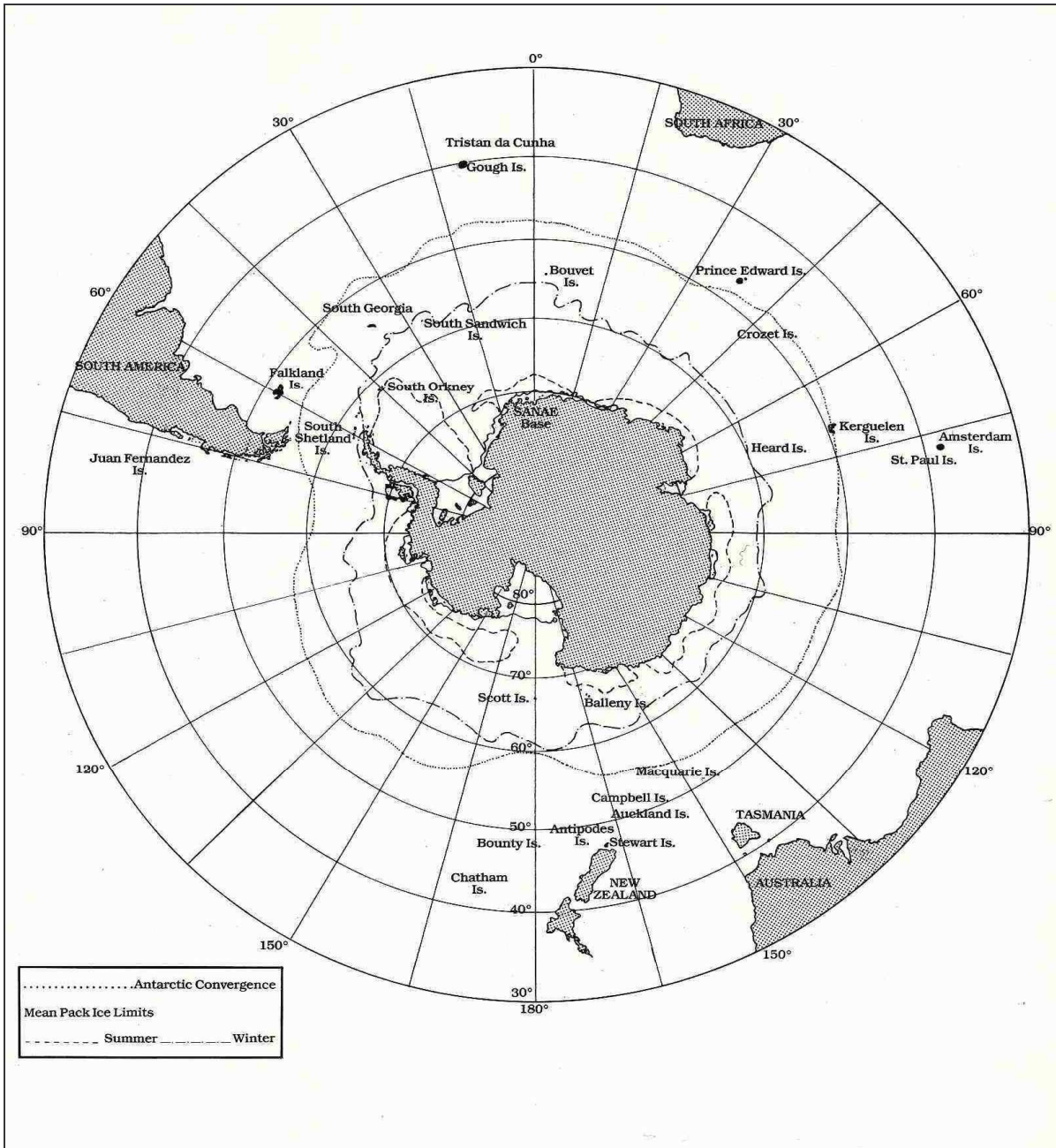
Elephant seals are true seals belonging to the family Phocidae (King 1983). Two species, similar in appearance and behaviour, and are separated mainly by range and timing of the breeding season (Bonner 1989; Ling & Bryden 1992) are extant. The northern elephant seal (*Mirounga angustirostris*) forages in the north-west Pacific Ocean (De Long *et al.* 1992, Stewart & De Long 1995) and hauls out to breed in the late boreal winter on islands off the coast of California and Baja California and at a few colonies on the California mainland (Bartholomew & Hubbs 1960; Stewart *et al.* 1994). The southern elephant seal inhabits the Southern Ocean and breeds in the austral summer. It is the largest of the Pinnipedia (King 1983) and is highly sexually dimorphic. The males are larger than the females (Figure 1.1), reaching 5m in length, compared to the 3m of females. Southern elephant seals can weigh up to approximately 3000 and 500 kg, for bulls and cows respectively (Carrick *et al.* 1962). Newborn pups weigh 40-46 kg and have a mean length of 1.27m (Laws 1994).



**Figure 1.1** Adult male and female elephant seals with a pup during breeding season, showing vastly different body sizes.

### 1.1.2 Distribution

Southern elephant seals (*Mirounga leonina*) have a circumpolar distribution in the Southern Ocean with major breeding populations close to the Antarctic Polar Front (APF) as shown in Figure 1.2 (Modified from Smithers 1983).



**Figure 1.2** The locations of southern elephant seal, *Mirounga leonina*, breeding populations (see appendix 2, table 1)

Laws (1960) proposed that the world population of southern elephant seals be divided into three sub-populations namely the Kerguelen stock (Îles Kerguelen, Heard Island, Prince Edward Islands, Îles Crozet), the South Georgia Stock (South Georgia, South Orkney Islands, South Shetland Islands, South Sandwich Islands, Gough Island, Bouvet Island, Valdés Peninsula, Falkland Islands) and the Macquarie stock (Macquarie Island, Campbell Island, Auckland Islands, Antipodes Islands). Recent genetic studies suggested that the Falkland Islands and Valdés Peninsula groups constitute a fourth southern elephant seal stock (Hoelzel *et al.* 1993). See figure 1.2 for the locations of these sites.

### **1.1.3 Life history**

Southern elephant seals exist pelagically for about 75% of their lives, spending the remaining time on land (Carrick *et al.* 1962) where they breed and moult during the austral spring and summer respectively (Condy 1979). Adults experience two haulouts per year. Breeding elephant seals are ashore from August to November, and return for the moult in December. Bulls are the first to arrive in early August and the first cows arrive about a month later in early September. Cows give birth approximately six days after hauling out (Condy 1979).

During the breeding season the cows are gregarious and form groups (Figure 1.3), though individuals are aggressive towards each other and adjacent cows never lie in contact. Bulls compete aggressively for access to the cows, driving off intruding competitors (Bonner 1989). The successful bull is known as a beachmaster. Groups containing more than 50-60 cows may include one or more additional bulls known as assistant beachmasters (Bonner 1989). A number of bachelors will lie in close proximity to the harem (Bester 1988). Defeated challengers as well as bachelor bulls (Condy 1979) often stay away from the breeding beaches, and they haul out in small inlets, coves, and on unoccupied beaches until the peak mating period. Cows are mated about 18 days postpartum with the peak mating period falling in late October and early November. The cows return to the sea 22-23 days after parturition when the pups are weaned (Condy 1979). During the peak mating period occasional changes occur in the bulls' status. After the peak in mating, the number of bulls hauled out on the breeding beaches declines, with bachelor bull numbers increasing towards the end of the mating season (Condy 1979; Bester 1990; Bester *et al.* 2001).



**Figure 1.3** A gregarious group of elephant seals during the breeding season at Marion Island. Adult female with unweaned pup in the foreground and an adult male (beachmaster) in the middle, with more females and pups in the background.

At the end of the breeding season adult seals go to sea for a few months, whereafter they return to land for the annual moult haulout (Figure 1.4). The moulting period lasts from November to the end of April and peaks in January and February for cows and bulls respectively. Each individual will moult for approximately 30 days (Condy 1979). Immature elephant seals have two haulouts per year. Yearlings haul out to moult in early November (Condy 1979), before the last of the breeding cows have departed. The first subadult males and females haul out to moult when the adults are departing at the end of the breeding season. Although both sexes arrive in early November, the number of subadult males increases more rapidly than females, so that the respective peaks are separated by approximately five weeks (Condy 1979), subadult males reaching peak numbers in mid-December.



**Figure 1.4** Southern elephant seals, *Mirounga leonina*, in the wallow at Marion Island during the moulting season.

Age accounts for much more of the temporal variation in moulting than does sex. Differences between the sexes vary among age classes. A difference in timing of the moult between females and males is first apparent amongst two-year-olds, the age at which some females fall pregnant for the first time (Kirkman *et al.* 2003). Reproduction evidently contributes to the shift in the timing of the female haulout from as young as one to four years of age in females, as pregnant two-year-old females moult later on average than virgins of the same age. The primiparous three-year-old females moult later on average than virgins of the same age. However, with pregnant females excluded, two-year-old females still moult later on average than males of the same age (Kirkman *et al.* 2003).

Between the moulting and breeding season, immature elephant seals of both sexes, and infrequently adults too, are known to haul out on one or more occasions for periods of a few days up to several weeks at a time. This is known as the winter haulout and its purpose is unknown (Laws 1956; Carrick *et al.* 1962; Odell 1974; Condy 1979; Stewart & Yochem 1984; Hindell & Burton 1988; Kirkman *et al.* 2001). A few subadults haul out during the winter, as do a few yearlings and underyearlings. However, by August, when the breeding bulls return for the next

breeding season, the numbers of overwintering seals decline, and by September when the cows start hauling out, very few immature seals remain on the island (Condy 1979).

Participation in the winter haulout differs between sexes, except among underyearlings (Kirkman *et al.* 2001). Within each sex, both age and reproductive history influence participation. Some individuals of both sexes participate even after they had attained breeding status. Participation between parous and non-parous females of the same age is similar. During the winter haulout there is no evidence that participation levels vary between cohorts or between years. But participation does differ between sexes, and within each sex, both age and reproductive status influences participation, with age the most important determinant (Kirkman *et al.* 2001). Elephant seals survive on stored energy during these haulout events (Laws 1956).

Underyearlings undergo two distinct terrestrial phases (Panagis 1981; Wilkinson & Bester 1990), a post-weaning phase before the final departure from the island in January, and a 'resting' phase when they return in March (Panagis 1981; Kirkman *et al.* 2003). The latter corresponds with the haulout of yearlings in March (Condy 1979) with many of these individuals overwintering (Panagis 1981). On Marion Island pups show limited movement from their natal beaches before departing from the island (Panagis 1981). The duration of the post-weaning fast increased linearly with an increase in weight at weaning in both males and females (Wilkinson & Bester 1990). Movement between the haulout sites during both the post-weaning phase and the resting phase is greater and more frequent in males than in females. Males frequently move greater distances between the sites in December than November, but during the winter haulout their movements are infrequent (Wilkinson & Bester 1990). Underyearling males are more inclined to disperse (locally) than older immature males when hauling out in winter at Marion Island (Hofmeyr 2000).

A little known aspect of the life history of the elephant seals is the level of intersite movement during haulout events and whether age, sex and reproductive status have any effect on the patterns and frequency of such movement, if present. Intersite movement refers to the movement of elephant seals between discrete beaches of an island during a haulout event. This study addressed this little understood aspect of the southern elephant seal terrestrial haulout.

## **1.2. Objectives of the study**

To establish the patterns and frequency of intersite movements of southern elephant seals in relation to age class, sex and haulout type.

To achieve the research objectives the following null hypotheses were tested:

1. Sex has no effect on either the frequency of movement, the distance moved or the number of sites visited by animals of different age classes during particular haulout events.
2. Age has no effect on either the frequency of movement, the distance moved or the number of sites visited by animals of different sexes during particular haulout events.
3. The type of haulout has no effect on either the frequency of movement, the distance moved or the number of sites visited by both male and female animals of different age classes.

The following key questions were posed as a means of testing the above hypotheses.

1. Does sex have an effect on either the frequency of times an animal moves between sites, the total distances it moves, or the number of sites it visits, all during a haulout event?
2. Does age class have an effect on either the frequency of times an animal moves between sites, the total distances it moves, or the number of sites it visits, all during a haulout event?
3. Does the type of haulout event affect either the frequency of times an animal moves between sites, the total distance it moves, or the number of sites it visits, during a haulout event?
4. Does the particular age of individuals within an age class affect either the frequency of times an animal moves between sites, the total distance it moves, or the number of sites it visits, during a haulout event?

## CHAPTER 2

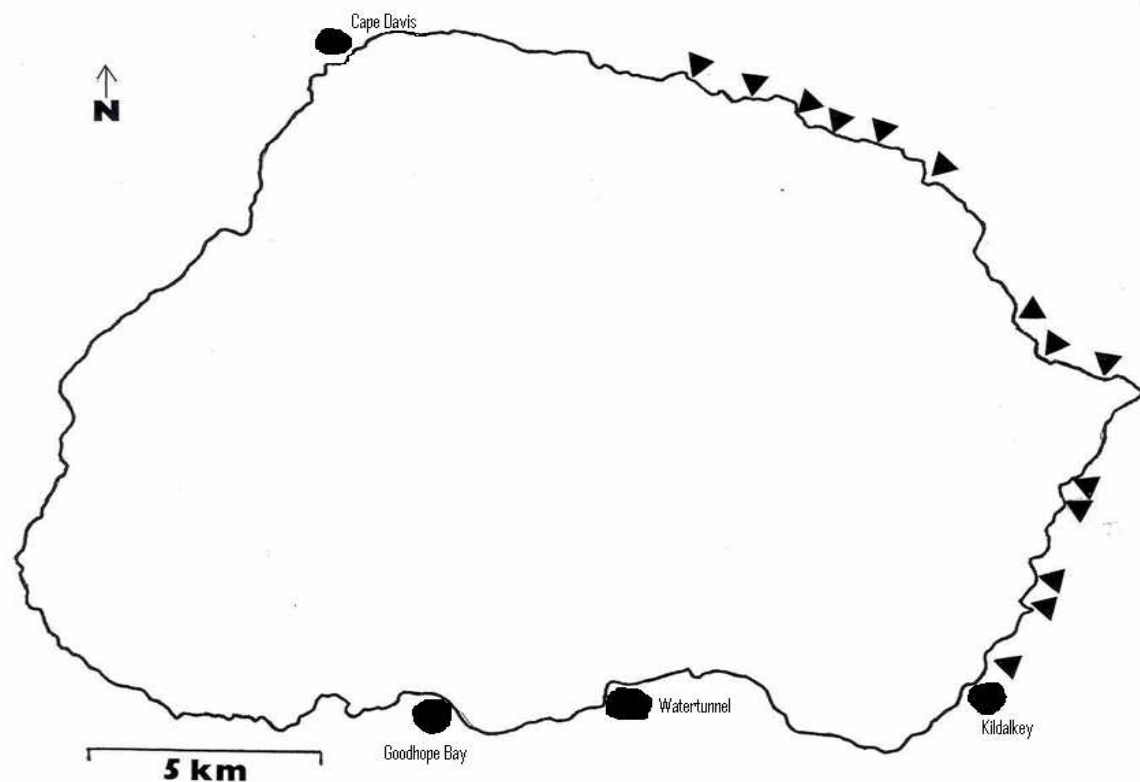
### STUDY SITE

#### 2.1 Location

Marion Island (46° 54'S, 37°45'E) is a Subantarctic island located in the southern Indian Ocean. It is one of two islands within the Prince Edward Islands group, which are situated approximately 2300 km south east of Cape Town, South Africa and 2100 km north of Antarctica (see Figure 1.2). Marion Island has an area of 290 km<sup>2</sup> and a coastline of approximately 87 km (Pistorius 2002). Prince Edward Island, which is 22 km away from Marion Island, has an area of only 80 km<sup>2</sup> (Verwoerd 1971, Wilkinson 1992). These islands are exposed to the same climatic conditions and are also similar in topography and the species they support (Verwoerd 1971).

#### 2.2 Topography

Marion Island is of volcanic origin (Verwoerd 1971) with a maximum altitude of 1230 metres (Mascarin Peak), and it measures 24 km from east to west and 17 km from north to south (Wilkinson 1992). The coastlines vary physiognomically, with cliff faces predominant and these cliffs are broken in a number of places by rough beaches. Elephant seals prefer hauling out on the sheltered northern and eastern coast beaches. These beaches lie between Cape Davis and Kildalkey Bay (Fig 2.1). On the south coast two further haulout sites are found, Watertunnel Beach and Goodhope Bay East (Condy 1977). Most of these beaches are made up of small rounded rocks, stones and pebbles (Wilkinson 1992). Only one sandy (Ship's Cove) and one shingle beach (Good Hope Bay) are found on the island.



**Figure 2.1** An outline of Marion Island, showing the northern and eastern beaches mostly preferred by elephant seals during haulout events. Cape Davis in the north to Kildalkey in the southeast, and Watertunnel and Goodhope Bay East in the south.

### 2.3 Climate

At Marion Island systematic meteorological observations have been made since the island was annexed from Britain in 1948 (Marsh 1948). The climate is basically marine with modifications due to the topography of the island itself (Schulze 1971). It is characterised by strong predominantly westerly winds with the highest velocity during the day and gales most frequent in the winter. Relatively low temperatures predominate with a mean annual temperature of 5.5°C with little annual or diurnal variation. Abundant precipitation is in the form of rain, snow or graupel (ice-rain) with an annual mean of 2576 mm. The humidity is relatively high (80%) with little annual or diurnal variation. Only 20 – 30% of the possible amount of sunshine reaches the island surface because of a high degree of cloudiness. Daylight duration is 15 h in summer and 9 h in winter (Schulze 1971; Wilkinson 1992). The mean annual sea surface temperatures measured at

the single research station are low (5.0°C) with little annual variation and are higher than the mean air temperatures during the winter months, from May to September (Schulze 1971). Instrumental data recorded at the South African Weather Service station on Marion Island shows that the local climate of this island has undergone significant changes since the 1960s (Smith & Steenkamp 1990), mostly during the austral summer. These include a decrease in rainfall, an increase in nonrainy days, changes in wind speed and direction, and an increase in maximum and minimum local air temperature and in near shore sea surface temperature (Rouault *et al.* 2005). It is suggested that the changes to the local climate of Marion Island are linked to the well-documented shift in phase of the semi-annual oscillation of tropospheric circulation in the Southern Hemisphere after about 1980 (Rouault *et al.* 2005).

## CHAPTER 3

### METHODS

#### 3.1 Data collection

The ongoing mark-resight program that had started in November 1983 at Marion Island (Bester & Wilkinson 1994; Pistorius *et al.* 1999a) generated the data analysed in this dissertation. Each breeding season, weaned pups were double tagged (Figure 3.1) in the webbing of their hind flippers with colour coded (indicating year of application, and hence cohort and age) three-digit numbered “Jumbo” rototags (Dalton Supplies Ltd, Henley-on-Thames) and sexed (Pistorius *et al.* 1999a). During each year beaches were censused on foot once a week during the breeding season and every ten days during the moulting season and resting phase (Kirkman *et al.* 2003).



**Figure 3.1** Adult elephant seal hind flipper with a tag in the webbing at Marion Island.

For each beach visited on each occasion, the following were recorded:

1. The number and colour combination of tags of tagged individuals.
2. The total number of adults (males separate from females),
3. The total number of subadults,
4. The total number of yearlings,
5. The total number of underyearlings,

6. The total number of pups (separated into dead and live, and pre-weaning and weaned),
7. The total numbers of animals on the beach.

For each of the five age classes above, the following were recorded:

1. Total number of seals of that age class,
2. Number of seals checked for tags,
3. Number of seals found with tags.

For each tagged animal found the following information were recorded:

1. Date of sighting
2. Site code,
3. Sex,
4. Tag colour combination (age),
5. Tag number,
6. Number of tags (one or two),
7. Social status,
8. Moulting stage.

Age group classification and sex identification of elephant seals at Marion Island followed Condy (1979). Classes are given below with class codes in parentheses.

Pups (P) = young animals of both sexes before the first pelagic excursion (00).

Underyearlings (UY) = animals of both sexes under the age of one year (10).

Yearlings (Y) = one-year-old animals of both sexes (20).

Subadults (SA) = males two years and older but younger than six years and females two years old (30).

Adults (A) = males six years and older and females three years and older (40).

All the data were entered and stored electronically in Microsoft Excel database files.

### **3. 2. Data selection and database**

Records of animals observed only once during a particular haulout and those observed only once after a period of five or more consecutive years were excluded from the data, to counter any

possible misidentification of individuals. Records of animals that were seen at other islands were also excluded. The database analysed for this study therefore only contained records of animals sighted two or more times during a specific haulout (See appendix 4), and only those sighted on Marion Island. All the data files from various years were pooled. A total of 19577 records were available for statistical analyses. Frequencies and percentages of number of sites visited, number of moves made and mean distances moved were determined from records for each age class, sex and each haulout event. A site that was re-visited by an animal on the move during a haulout was considered a new site, and the distance moved was calculated as the cumulative addition of total the distance moved from one site to another (Hofmeyr 2000). The distances from one site to another were measured from the centre of each site.

### **3.3. Statistical analysis**

ANOVA, from the SAS version 8.2 statistical package, was used to determine if there was difference among the variants in number of times moved, number of sites visited and the distance covered by elephant seals of different age classes, sexes and haulout types. Where there was difference a further post-hoc test was done using Scheffe's Multiple Comparison method and/or the LS Means to test the pairwise difference.

### **3.4. Limitations and assumptions**

For convenience, elephant seals were assumed to age by a year on 15 October each year, the date of peak number of breeding females at Marion Island (Wilkinson 1992). However, for ease of handling the data, a year was added onto the age of all tagged seals at their first resighting during the breeding season, even if they were resighted before the median birth date (15 October). This was done so that a breeding animal would have only one age during a particular breeding season (Hofmeyr 2000).

While male elephant seals generally attain sexual maturity at the age of five, and attain social maturity at the age of eight (Laws & Le Boeuf 1994), in the small Marion Island population they are able to hold harems as early as the age of six (Pistorius *et al.* 2001). Bulls of age six that have been recorded present during the breeding season were considered adult (40) but the rest of six-year-old males were still considered subadult (30) following Kirkman *et al.* (2003). The youngest females to give birth at Marion Island were three years old (Bester & Wilkinson 1994), but any

female age three and older was considered adults (40), whether they have been observed with pups or not.

Tags were assumed to have been read correctly. There were some problematic records in the database, for example, males identified (erroneously) as such at weaning, being recorded on occasion as females with pup. Animals recorded once after an absence of many years were of more concern, and obviously these aberrant records have been excluded from the database. Such records were few, testimony to the high standard of fieldwork done by observers (Hofmeyr 2000).

It is assumed that the intensity and efficiency of search efforts during the study period was consistent, irrespective of the changes in observers, weather or seasons (Hofmeyr 2000). As the present mark-recapture programme is based on a rigorous resighting protocol, we expect that if any bias occurred that it would have been constant throughout the study period (Pistorius & Bester 2002). The exact times and dates of arrival and departure of elephant seals at the sites could not be recorded as the resights could not be done at daily intervals (Pistorius *et al.* 1999).

The moulting season extends from one calendar year to another. To enable the pooling of all the moulting data, and to assign moulting animals to a particular year, the moulting data from January to May of each year were backdated by one year, e.g. animals moulting from January to May 2000 become the moulters of 1999 (Hofmeyr 2000).

From 1983 to 1989, census and hence tag resights, took place only from August of one year to the May of the next year, which means that the winter haulout went largely unrecorded. Complete winter records were therefore only available from 1990 onwards.

## CHAPTER 4

### THE INFLUENCE OF AGE CLASS, SEX AND HAULOUT TYPE ON THE PATTERN AND FREQUENCY OF LOCAL MOVEMENTS BY SEALS

#### 4.1 Introduction

This chapter explains the influence of sex, age class and haulout type on local movement in terms of the number of times moved, the number of sites visited and the distances travelled by southern elephant seals between sites at Marion Island. The age class and sex comparisons were made for all three measures of movement. Comparisons were done between males and females only of corresponding age class (i.e. between male and female underyearlings, yearlings, etc.), as well as between different age classes within each sex.

#### 4.2 Results

##### 4.2.1 Number of moves

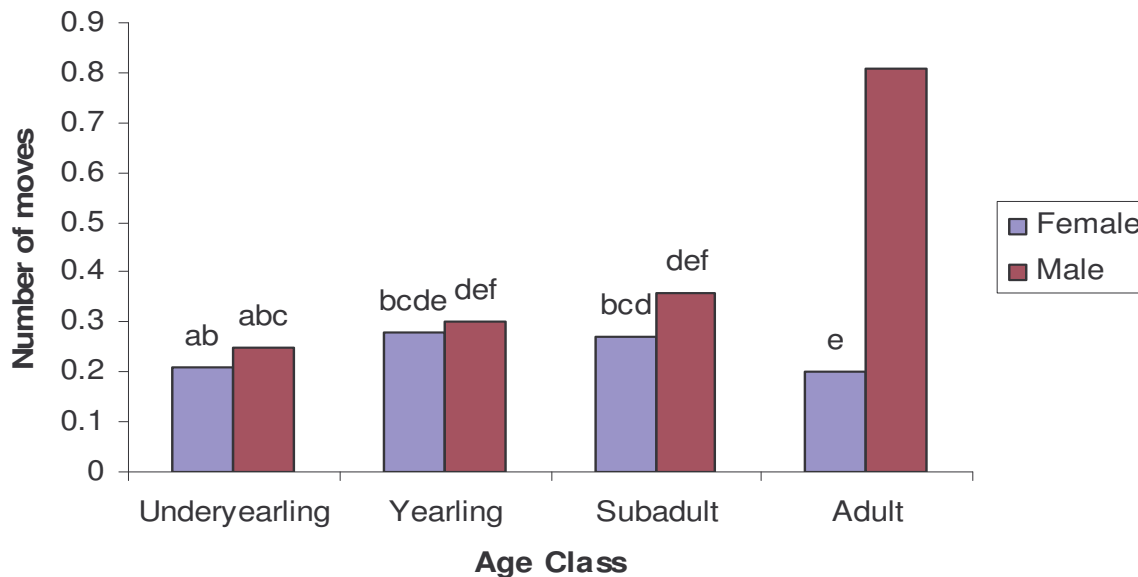
Southern elephant seals of both sexes and all age classes, except the males during the breeding season haulout, moved less than once on average during all types of haulouts. All the results of the ANOVA tests are detailed in Appendix 5, Table 13. Interactions between age class and sex ( $F = 52.01$ ,  $DF = 3$ ,  $P < 0.0001$ ) and haulout type and sex ( $F = 13.88$ ,  $DF = 3$ ,  $P < 0.0001$ ) were significant, but not those between haulout type and age class ( $F = 3.96$ ,  $DF = 1$ ,  $P = 0.0465$ ).

##### *Age class and sex*

When considering the number of times southern elephant seals moved on average during a haulout, there was a significant interaction between age class and sex (Figure 4.1). Females generally moved very seldom during a haulout, on average less than 0.3 times (Appendix 3, Table 2). They showed little change in the number of these moves over the course of their lives. While adult females on average moved less (0.2 times during a haulout) than females of all other age classes, this was only significant when compared to underyearlings (0.21 times) and subadults (0.27 times). There was a clear pattern shown by male elephant seals in number of moves made during a haulout with respect to different age classes. Male elephant seals also moved on average less than once

during a haulout, but the actual number changed significantly with age. Adult males moved two to four times more often than all other male age classes. Underyearlings moved significantly less (0.25 times) often than all other age classes (Y = 0.3 times, SA = 0.36 times, A = 0.81 times).

There was no significant difference between males and females in the number of times an individual moved during a haulout when considering underyearlings, yearlings or subadults, but adult males moved significantly more often (> 4 times) than adult females.



**Figure 4.1** Mean number of intra-haulout site moves, for all haulouts, by male and female southern elephant seals of various age classes at Marion Island. Means labelled with a common character (a, b, c, d, e, f) do not differ significantly.

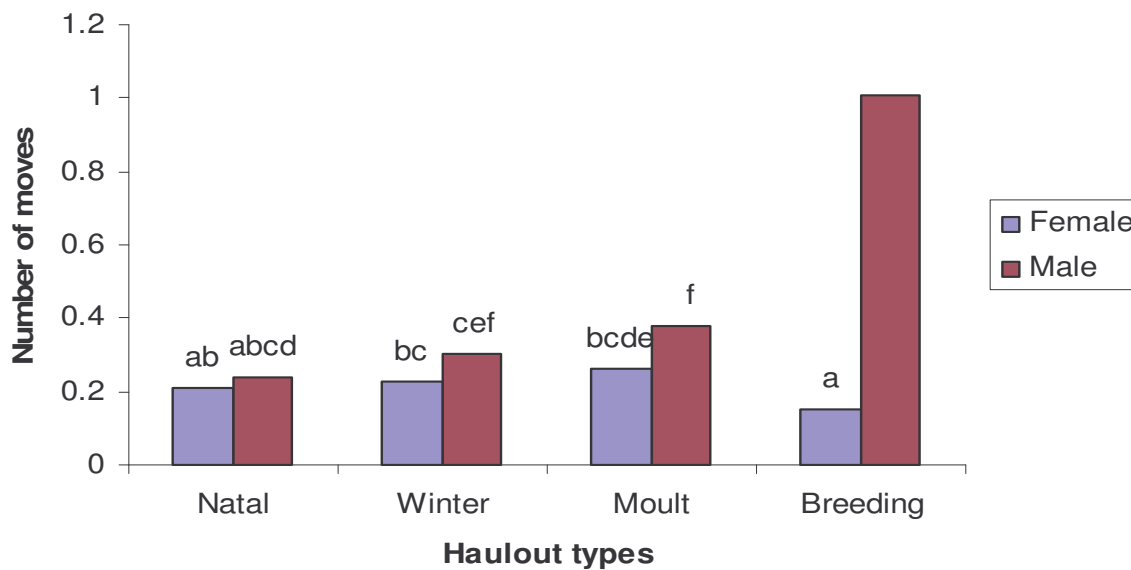
#### *Haulout types and sex*

Females showed little pattern in the number of times moved during a single haulout when considering different types of haulout (Figure 4.2). On average, breeding females moved less often (0.15 times) during a haulout than those ashore for other types of haulouts (Appendix 3, Table 3). This was significant only when compared to the moult (0.26 times) and winter (0.23 times) periods but not the natal period (0.21 times).

There was clear pattern in the number of times that male elephant seals moved during a single haulout, with respect to the different haulout types. There was no significant difference in the

number of times moved between wintering (0.3 times) and moulting (0.38 times) males, but males moved significantly less during the natal period (0.24 times) than during all other haulouts. Breeding males moved at least once on average, which was significantly more often than for all other types of haulouts.

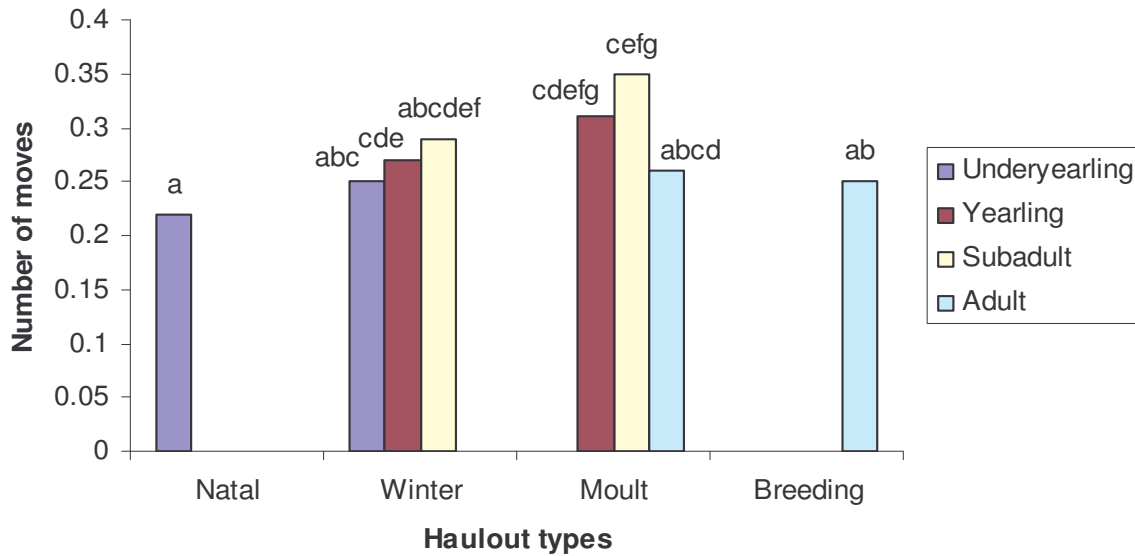
There was no significant difference between males and females in the number of times seals moved during natal and winter haulouts, but males moved significantly more often during the moult (males = 0.38 times, females = 0.26 times) and breeding haulout (males = 1.01 times, females = 0.15 times).



**Figure 4.2** Mean number of intra-haulout site moves by male and female southern elephant seals of all age classes during different types of haulouts at Marion Island. Means labelled with a common character (a, b, c, d, e, f) do not differ significantly.

#### *Haulout types and age class*

There was no significant interaction between age class and haulout types with respect to the number of times southern elephant seals moved during a particular type of haulout (Figure 4.3).



**Figure 4.3** Mean number of intra-haulout site moves by southern elephant seals of various age classes during different types of haulouts at Marion Island. Each age class includes both males and females. Means labelled with a common character (a, b, c, d, e, f, g) do not differ significantly.

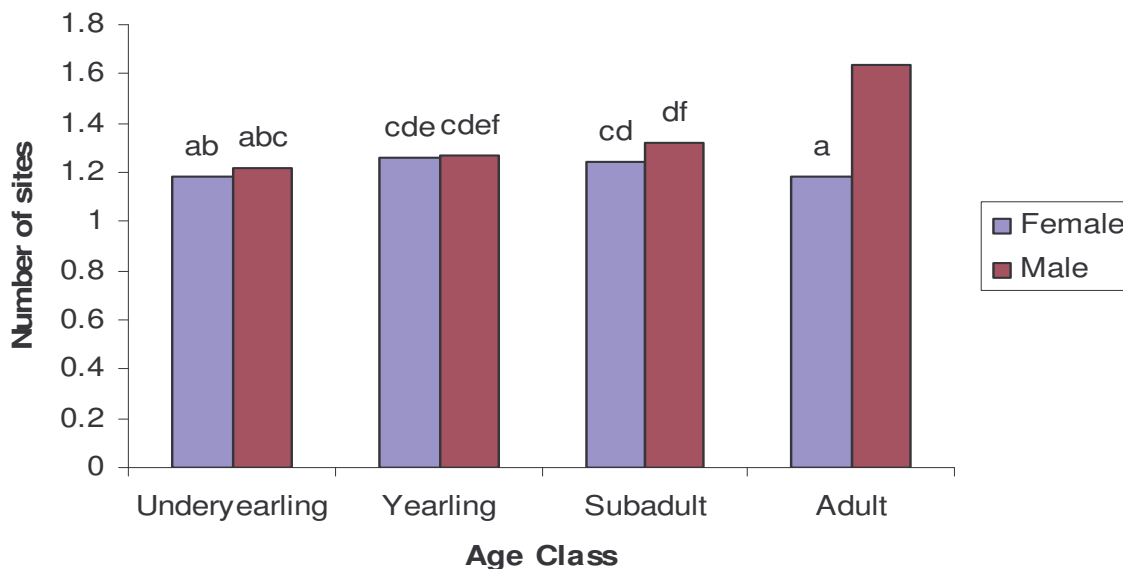
#### 4.2.2 Number of sites

Southern elephant seals of both sexes and all age classes visited less than two sites on average during all types of haulouts. For results of the ANOVA tests see Appendix 5, Table 14. The interactions between age class and sex ( $F = 50.80$ ,  $DF = 3$ ,  $P < 0.0001$ ) and haulout type and sex ( $F = 8.67$ ,  $DF = 3$ ,  $P < 0.0001$ ) were significant, but those between haulout type and age class were not significant ( $F = 3.63$ ,  $DF = 1$ ,  $P < 0.0568$ ).

#### *Age class and sex*

When considering the number of sites southern elephant seals visited on average during a haulout, there was significant interaction between age class and sex. Generally females visited few sites during any one haulout, on average less than 1.26 (Appendix 3, Table 5). While they showed little change in the number of these sites used within any one haulout over the course of their lives, both underyearling (1.18) and adult (1.18) females visited significantly less sites on average than both yearlings (1.26) and subadults (1.24).

Male elephant seals also showed a clear pattern in the mean number of sites visited during any one haulout over the course of their lives, but this was different from the pattern shown by females (Figure 4.4). Male elephant seals visited on average less than two sites during a haulout. Adult males visited significantly more sites on average (1.64) than all other male age classes, while underyearlings visited fewer sites (1.22) than other age classes ( $Y = 1.27$ ,  $SA = 1.32$ ), but this was only significant when compared to subadults. While there was no significant difference between males and females in the number of sites visited during a haulout by underyearlings, yearlings and subadults, adult males visited significantly more sites (1.64) than adult females (1.18).

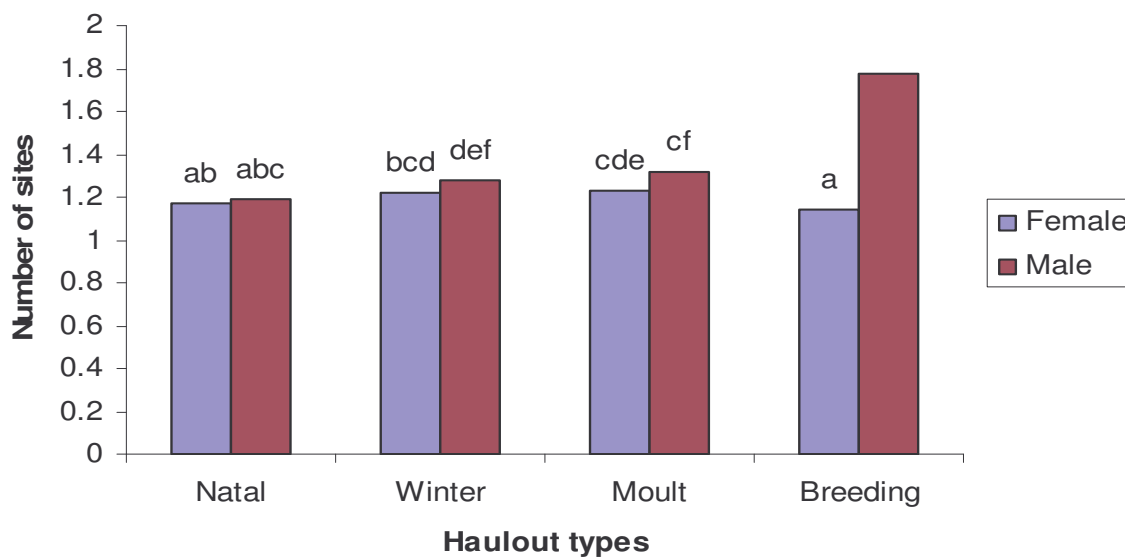


**Figure 4.4** Mean numbers of sites visited during a single haulout by male and female southern elephant seals of all age classes at Marion Island. Means labelled with a common character (a, b, c, d, e, f) do not differ significantly.

#### *Haulout types and sex*

There was little pattern shown by females in the mean number of sites visited during a haulout for the different haulout types (Figure 4.5). On average, breeding females visited fewer (1.14) sites during a haulout than all other haulout types (natal = 1.17, winter = 1.22, moult = 1.23) (Appendix 3, Table 6). This was only significant when compared to winter and moult haulouts, but not the natal period. There was no significant difference in the number of intra-haulout sites visited between the females ashore during the natal period, and those engaged in a winter haulout.

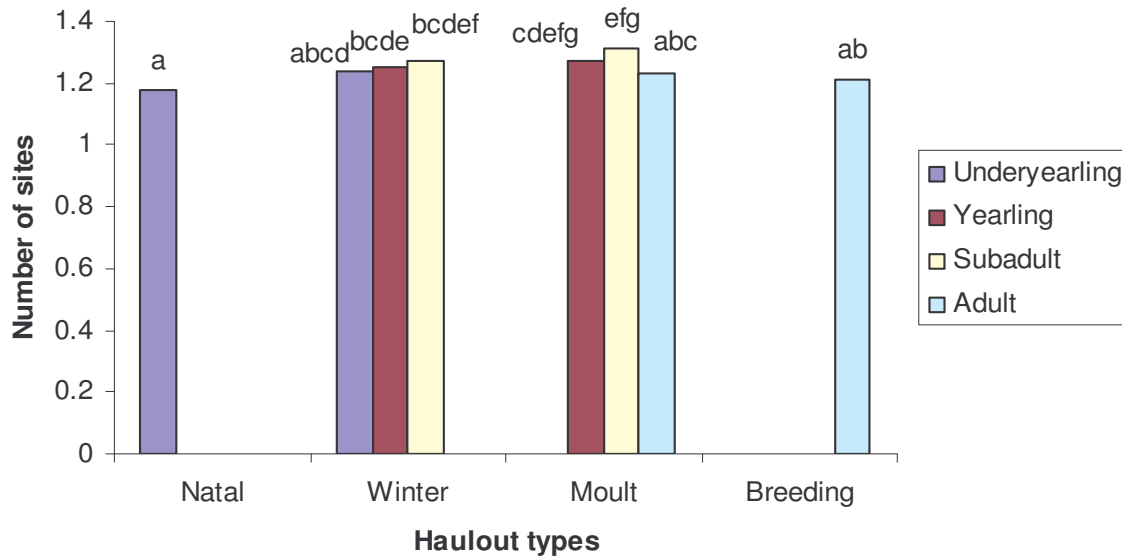
There was a clear pattern shown by male elephant seals in the number of sites visited during a haulout for the different haulout types. There was no significant difference in the number of sites visited between wintering (1.28) and moulting (1.32) males, but on average male elephant seals visited fewer sites during the natal period (1.19) than during all other haulouts. This was only significant when compared to winter and breeding haulouts. On average breeding males visited significantly more sites (1.78) than males ashore for all other haulout types. There was no significant difference between males and females in the number of sites visited during natal, winter and moult haulouts, but males visited significantly more sites than females during the breeding haulout (male = 1.78, female = 1.14).



**Figure 4.5** Mean numbers of sites visited in a single haulout by male and female southern elephant seals during different types of haulouts at Marion Island. Means labelled with a common character (a, b, c, d, e, f) do not differ significantly.

#### *Haulout types and age class*

There was no significant interaction between age class and haulout type with respect to the number of sites visited during a haulout (Figure 4.6). There was no significant difference in number of sites visited by seals of the different age classes during different types of haulout except for the moult. When considered individually only one significant interaction was found, with subadults visiting significantly more sites on average (1.3) than adults (1.23) (Appendix 3, Table 7).



**Figure 4.6** Mean numbers of sites visited during a single haulout by southern elephant seals of all age classes during different haulout types at Marion Island. Each age class includes both males and females. Means labelled with a common character (a, b, c, d, e, f, g) do not differ significantly.

#### 4.2.3 Distance

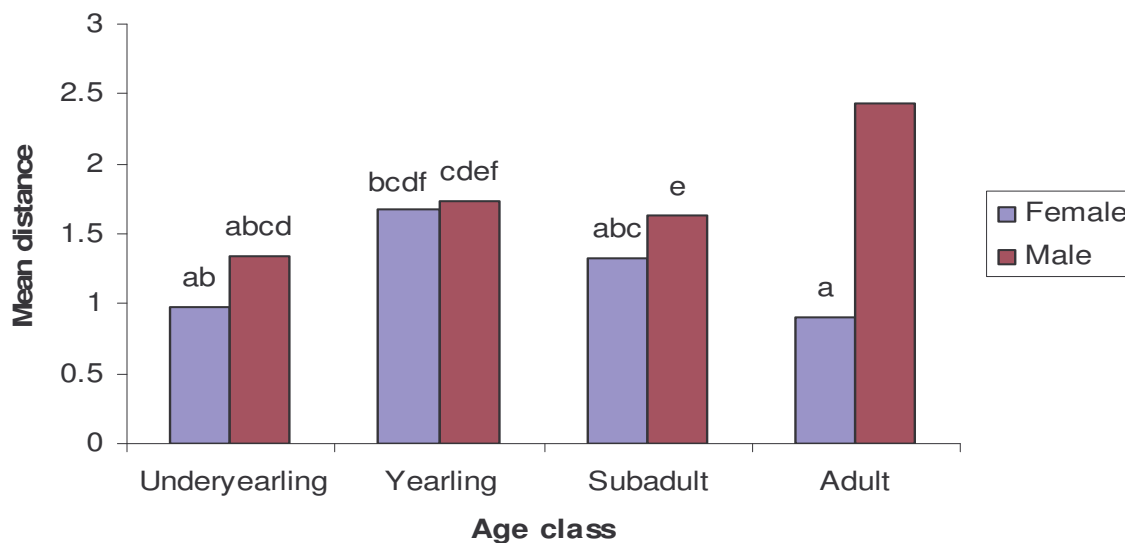
Southern elephant seals of both sexes and all age classes moved less than 3 km on average during all types of haulouts. ANOVA (SAS, Procedure GLM) was employed to determine if sex, age class, haulout type and their interactions have an influence on the distance moved (See Appendix 2, Table 15). The interactions between age class and sex ( $F = 24.61$ ,  $DF = 3$ ,  $P < 0.0001$ ) and haulout type and sex ( $F = 4.35$ ,  $DF = 3$ ,  $P < 0.0001$ ) were significant, but the interaction between haulout type and age classes ( $F = 1.37$ ,  $DF = 1$ ,  $P = 0.2414$ ) was not significant.

#### *Age class and sex*

The results showed a significant interaction between age class and sex with respect to the mean distance moved during a haulout. For females, little or no pattern was shown (Figure 4.7) in the distance moved during haulouts over the course of their lives, although adult females moved a shorter distance on average (0.91 km) than all other age classes (UY = 0.98, Y = 1.67 km, SA = 1.33) (Appendix 3, Table 8). This was only significant when compared to yearlings.

On the other hand, male southern elephant seals showed a clear pattern in the distance moved during haulouts over the course of their lives. Adult males move significantly further (2.43 km) than all other age classes (UY = 1.34 km, Y= 1.75 km, SA= 1.63 km). While underyearlings moved a shorter distance than other age classes, this was only significant when compared to subadults.

There was no significant difference between the haulout distances moved by male and female underyearlings or yearlings; but males moved significantly further than females, as subadults (males = 1.63 km, females = 1.33 km) and as adults (males 2.43 km, females = 0.91 km).

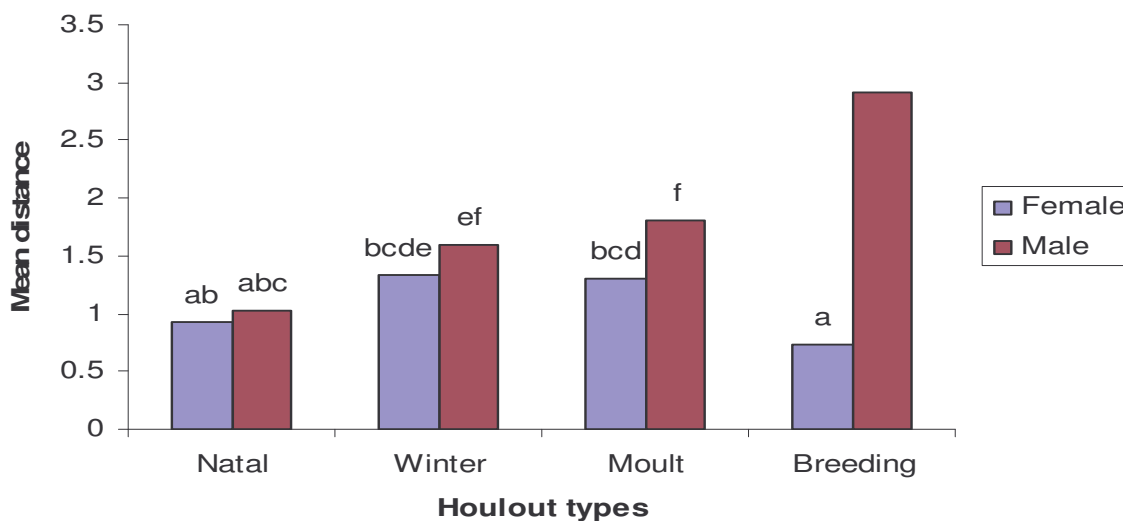


**Figure 4.7** Mean distances moved during all types of haulout by male and female southern elephant seals of various age classes at Marion Island. Means labelled with a common character (a, b, c, d, e, f) do not differ significantly.

#### *Haulout types and sex*

There was significant interaction between sex and haulout type with respect to the average distance moved during a haulout. Females showed little obvious pattern in distance moved during different haulout types (Figure 4.8). On average breeding females moved a significantly shorter distance (0.73 km) compared to females during both the winter (1.33 km) and the moult haulout (1.59 km) (Appendix 3, Table 9). There was no significant difference between the distances moved by females during the breeding and the natal haulouts (0.92 km).

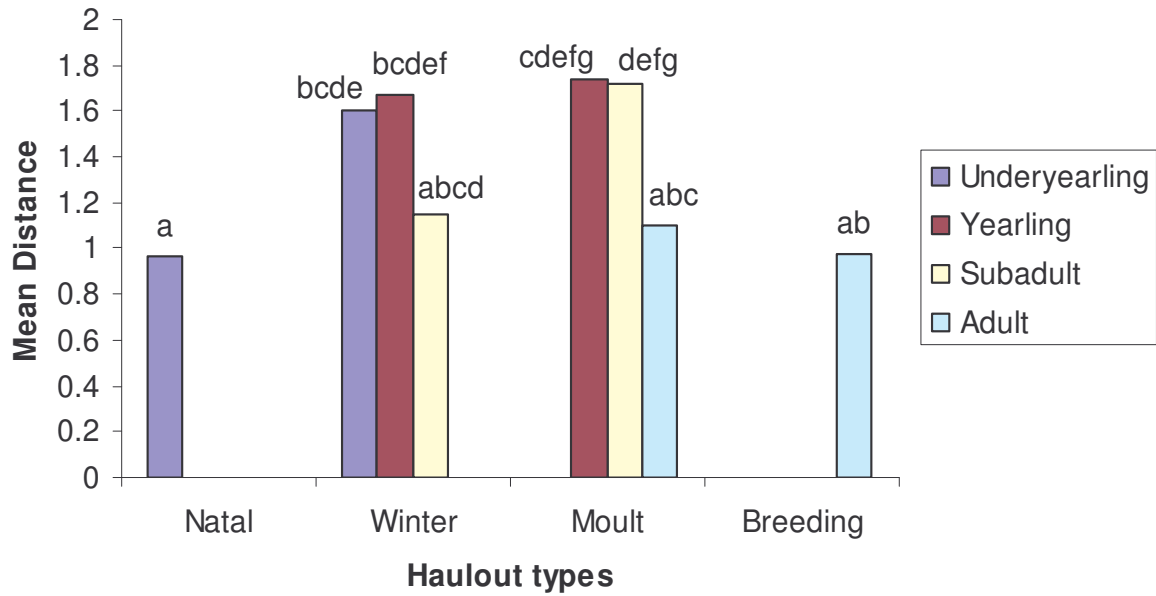
There was a clear pattern in haulout distance moved by males during different haulout types. There was no significant difference between the distances moved by males during the winter (1.59 km) and the moult haulout (1.81 km), but during the natal period males moved significantly shorter distances (1.02 km) than during all other types of haulouts. Breeding males moved significantly further (2.91 km) than males hauled out for other reasons. There was no significant difference between males and females in distance moved during the natal and the winter haulouts. However, males move significantly further than females during the moult (males = 1.81 km, females = 1.59 km) and also during the breeding haulout, where males (2.92 km) moved three times further on average than females (0.73 km).



**Figure 4.8** Mean distances moved by male and female southern elephant seals of all ages during different haulout types at Marion Island. Means labelled with a common character (a, b, c, d, e, f) do not differ significantly.

#### *Haulout types and age class*

There was no significant difference in the distance moved during a haulout between haulout types by animals of a particular age class, except in two cases. Underyearlings moved significantly further during the winter haulout (1.60 km) than when ashore after weaning (0.97 km) (Appendix 3, Table 10). Also moulting adults moved a shorter distance (1.10 km) on average than other age classes (Y = 1.74 km, SA = 1.72 km), but this was only significantly different when compared to subadults (Figure 4.9).



**Figure 4.9** Mean distances moved by southern elephant seals of various age classes during different types of haulouts at Marion Island. Each age class includes both males and females. Means labelled with a common character (a, b, c, d, e, f, g) do not differ significantly.

### **4.3 Discussion**

Movements of elephant seals of different age classes and sexes during a particular haulout were measured during this study in three different ways. Firstly, by the number of times a seal moved during a haulout, secondly by the number of sites that a seal visited during a haulout, and thirdly by the distance each seal moved during a haulout. The results of all three types of measurement were broadly similar and will therefore be discussed together for each of the three comparisons (age class and sex, haulout type and sex, and finally, age class and haulout type). It must also be noted that, in each case, analysis of the data was limited to a two-way comparison and the data was not broken down using all three categories. For example, when breaking down the data by age class and sex, the resulting categories (adult males, adult females, subadult males, etc) each included data from two types of haulouts (breeding and moulting for adults, moulting and winter for subadults, etc). This method of analysis has affected the results shown and is relevant to this discussion.

#### **4.3.1 Age class and sex**

For none of the classes of immature (underyearlings, yearlings and subadults) elephant seals was any significant difference shown between males and females in the mean number of times elephant seals moved between sites and also, in the mean number of sites that they visited during a haulout. Since none of the animals belonging to these age categories take part in breeding, it was quite possible that there were no marked differences between the sexes in their way of life. For the third means of measurement, distance travelled, only for underyearlings and yearlings were no significant differences between the sexes shown. In common with the pattern for adults, subadult males moved significantly further than subadult females. This showed that, although participation in the breeding haulout may be important in determining differences in their way of life, it was not the only important factor. Other issues may be important.

Both male and female underyearlings were still inexperienced and were relatively poor swimmers and divers (Wilkinson & Bester 1990), which is probably why there was no significant difference between the sexes. Absence of difference was contrary to that found by a previous study in which male underyearling elephant seals at Marion Island showed a greater tendency to change location than did females (Wilkinson & Bester 1990). The authors suggested that this was due to the greater weaning weight of males. This would allow them to spend more time in the vicinity of the island

before their first extended foraging trip, and thus increase the time over which movements could be recorded. However, the number of occasions individuals changed site did not differ between sexes in the previous study, and underyearlings of both sexes moved less than a kilometre (Wilkinson & Bester 1990), a result similar to the findings of the present study.

In this study, differences between subadult males and females were expected, because of differences in the age range of each class. But this was only evident for the distance travelled, where subadult males moved significantly further than females. However, even though subadult males may include older animals (generally ages two to five) than subadult females (generally two years old) (Carrick *et al.* 1962b) and are much larger, it was possible that their behaviour ashore was no different, perhaps because terrestrial requirements during the moult and winter at this age are presumably the same (Carrick *et al.* 1962a).

As was expected, a major difference between adult males and females was evident in this study. This age class comprises of matured individuals that haul out for both the moulting and the breeding seasons. While the two sexes may behave in similar manner during the moult with a similar sequence of hair shedding (Carrick *et al.* 1962a; Condy 1979), they behave very differently during the breeding season. In the breeding season females were ashore for approximately one month, during that time suckling their pups for  $\pm 23$  days (Carrick *et al.* 1962b; Condy 1978; Wilkinson 1992). Pups cannot move far and cannot swim, which limits the movement of their mothers to the period outside lactation. Bulls were ashore for a longer period than any other class (up to three months) (Condy 1979; Wilkinson & Bester 1990; Kirkman 1999), which gave them more time to move between the sites. During this time they compete with each other and may be forced to move considerably more in order to search for unaccompanied cows, or to escape after aggressive interactions (Carrick *et al.* 1962b). In addition, males were not limited by the need to care for a relatively immobile pup (Carrick *et al.* 1962a).

At Marion Island female elephant seals generally moved very seldom during a haulout. As was expected adult females moved less, visited fewer sites, and consequently moved a shorter distance than females of all other age classes. This group comprised of matured individuals (some 3-year-olds, a large proportion of 4- and 5-year-olds, and most females older than 6 years) (Condy 1979) that participate in both the breeding and moulting haulouts. Condy (1979) also indicated that yearling and subadult females have greater tendency to wander between sites. These age classes of females were able to do so because they have no dependant pups. The general lack of a significant

difference between adult females and underyearlings ashore after birth was not surprising, since they spend the majority of their time ashore together. The only significant difference between these two age classes was in the number of moves recorded between sites. It was possible that the difference recorded here was because the two categories include haulouts other than the breeding and natal periods ashore (winter in the case of underyearlings, and moult in the case of adult females). Differences in their behaviour ashore during these two periods are likely given differences in the ages of the animals concerned.

Just like their female counterparts, adult males were involved in both the breeding and moult haulouts. During the breeding season bulls compete with each other for the control of breeding beaches (Condy 1979). While defeated challengers and other bachelor bulls may remain on the breeding beaches during the peak mating period, they were found on the periphery of the harems. During these periods changes in bulls' status do occur occasionally (Condy 1979). As a result of these, bulls moved between breeding beaches trying to access cows elsewhere. This was likely the cause of adult male elephant seals at Marion Island moving more than two to four times that moved by males of all other age classes and covering a mean distance of 2.43 km. Underyearling males moved less and visited fewer sites than other age classes. Wilkinson & Bester (1990) and Panagis (1981) noted that immature seals were relatively sedentary during the post-weaning period and winter haulout for the population at Marion Island. At Îles Kerguelen, however, more extensive movements have been recorded for underyearlings on the Courbet Peninsula during the post-weaning period. These differences may be linked to the different physiognomy of the beaches at the latter site. The Courbet Peninsula has almost continuous open, sandy and pebble/boulder beaches, whereas Marion Island has well demarcated small beaches with headlands and interspersed with non-negotiable stretches of coastline. The physiognomy at Marion Island seems to impede movement, as underyearlings seemed reluctant to negotiate deeper water without available hauling out sites on the adjacent coastline (Wilkinson & Bester 1990) as did underyearlings on certain sections of coast on the Courbet Peninsula (Lenglart & Bester 1982).

#### **4.3.2 Haulout types and sex**

Females ashore during the breeding and natal periods moved less and visited fewer sites than females ashore during the moult and winter periods. Adult females hauling out during the breeding season also moved shorter distances than females engaged in other haulouts. This difference was possibly due to the different obligations that the different age categories of females were subject to

during each type of haulout. The time period during which breeding adult females moved was limited to a few days before parturition ( $\pm 6$  days) (Carrick *et al.* 1962a; Condy 1979), and a few days after weaning ( $\pm 3.5$  days) (Condy 1979). These periods must be of limited duration since cows need to reserve their stored energy for suckling their pups. Carrick *et al.* (1962a) observed a cow that had lost her pup after hauling out 15 days pre-partum. Her food reserves had been depleted to such an extent by the initial fast that she failed to meet the strain imposed by lactation. Other species of seals were subject to similar limitations. For example, female grey seals tend to remain with their pup for the duration of a 17-day lactation period (Twiss *et al.* 1994).

Seasonal changes in the occurrence of killer whales off Marion Island may also have an impact on movements by elephant seals. Killer whale sightings increased greatly in number from October to the end of December, during the elephant seal breeding season, after which there was a decline in January (Condy *et al.* 1978; Keith *et al.* 2001). Killer whales patrol the island coastline intensively during the breeding season (Pistorius *et al.* 2002). At Marion Island movements between beaches by elephant seals require them to enter water deep enough for killer whales to access. Both adult females and underyearling elephant seals may therefore minimise swims close inshore at these times, which may result in them reducing the frequency of movements between sites, with most of the seals moving only once and covering a distance of less than a kilometre before leaving the island (Wilkinson & Bester 1990; this study). Apart from a small increase during the period from late April to early May, killer whales were largely absent from the island outside of the breeding season (Keith *et al.* 2001), and so would conceivably not affect dispersion patterns of elephant seals frequenting the island at this time.

Female elephant seals, like the males, undergo three different phases during the moult haulout: the pre-moult, the actual moult itself and the post-moult phases (Carrick *et al.* 1962a). During the pre- and post-moult phases they were far less reluctant to move between sites. During the middle phase, however, seals avoided going to the sea. It was during this time that their old pelage and skin was being replaced by a new one and was therefore flushed with blood to promote its growth (Laws 1956a). Carrick *et al.* (1962a) found that while immature females at Macquarie Island may change location during any phase of the moult, they generally complete all three phases at the same place. Both wintering and moulting females moved further than those ashore for other haulout types, but these were only significant when considering adults. This was because adult females take part in breeding haulouts, which require them spending most of the time nursing their pups, whereas during the moulting period any seal may change sites more readily. The reduction in killer whale

numbers seen at Marion Island during the moulting season may also encourage movement between sites. Another contributing factor was that both mature (adults) and immature (yearlings & subadults) animals take part in the moult haulout. But this was not the case for the winter haulout as mostly immature animals took part, and during this period seals may also change location (Carrick *et al.* 1962a).

The number of times male animals moved and visited a site increased as they became more mature and more experienced. As with females, post-weaning males ashore during the natal period moved very little, visited fewer sites and moved shorter distances during this period ashore than other haulout types. It was assumed that there are few differences in the life history and requirements of male and female underyearlings and therefore likely to show the same behaviour (Modig *et al.* 1995). Except for participating in mock fights, Modig *et al.* (1995) observed no differences in behaviour of male and female pups, and both sexes spent equal time resting. However, Wilkinson and Bester (1990) found that males moved more than females. The small number of moves made, fewer sites visited and shorter distance moved during the natal period by male elephant seals relate to their immaturity and inexperience. During this period they spend most of their time perfecting their swimming skills and losing weight before engaging in long distance movements (Wilkinson & Bester 1990). On the other hand, breeding males moved more and visited more sites than did males ashore during other haulout types. They also moved over longer distances than during other haulout types. As mentioned previously these results were expected, because males compete with each other for breeding beaches and access to females during the breeding haulout (Carrick *et al.* 1962a; Condy 1979). Where males are unsuccessful at obtaining control of a harem they often move elsewhere in an attempt to find mating opportunities (Condy 1979).

Differences between the sexes become especially apparent in the winter and moult haulout of both subadults and adults. We therefore assumed that males and females of these groups have different requirements with Laws (1956a) reporting that it is only the male elephant seals that may feed a little during the moult. A short visit to the water may result in male elephant seals changing location more often and moving longer distances than the females. The great difference in behaviour between males and females during the breeding season, however, relates partially to differences in the requirements of each sex during this time of the year. Males require mating opportunities, while females require a good site to give birth and suckle pups (Galimberti *et al.* 2000b). Mating opportunities were of less concern to females since males will expend energy finding them. Therefore during the breeding haulout bulls moved and changed location more often

because of the competition for mating opportunities. This movement may help them to access females, or to access more females, and that the increased chance of finding females was worth the risk of predation by killer whales during this period. In addition, adult male elephant seals may also be less susceptible to predation due to their large size. As a result of these factors males tend to cover longer distance than females during the breeding haulouts.

#### **4.3.3 Haulout types and age class**

The present study showed no significant interaction between haulout types and age class. Although the relationships among age classes were not significantly different during the winter, the number of times animals of a particular age class moved increased with maturity. During the winter and moult haulout subadults moved further and visited more sites more often than other age classes. But this was only significant when compared to moulting adults in terms of number of sites visited during a haulout. Carrick *et al.* (1962a) found that immature seals at Macquarie Island were mostly widely dispersed during their second year of life. These dispersion maybe the course of difference in number of times moved between this class and other age classes during the winter and moult haulout.

As it was expected, subadults covered a greater distance than adults during the moult haulout. The nature of the previous haulout each of these age classes were involved in may be of relevance. Participation in the tough and energy taxing breeding season would have required adults to be more conservative with their movements during the subsequent haulout so as to conserve energy. On the other hand the previous haulout for subadults was the winter haulout, which was possibly a resting phase (Carrick *et al.* 1962a). McCann (1982) found that variations in activity patterns were related to the costs and benefits involved. Therefore subadults may have more energy reserves available to spend on movement than adults. Another possible reason might be the preference site of haulout during this period, as adults preferred wallows where they completed all three phases of moult at the same place. Unlike subadults that preferred moulting on the beaches and were likely to change sites during any phase (Carrick *et al.* 1962a). Though the difference was not significant, subadults moved over shorter distances and visited fewer sites than yearlings and underyearlings during both wintering and moulting haulout.

#### **4.4 Conclusion**

It can therefore be concluded that both males and females elephant seals show a pattern of movement in all three measures. There is no sex bias in all three measures of movement by immatures, except for the distance where subadult males travelled further than subadult females. For adult elephant seals, males moved more and travelled further than females during the moult and breeding seasons. There is no significant difference between the various classes of immature elephant seals in all three measures of movement. Breeding males moved more, visited more sites and travelled further than seals of all other age classes in all three measures of movement. This is because males are mostly involved in fight interaction for the access of females during this haulout. Breeding females moved less, visited fewer sites and travelled shorter distances than seals of all other age classes. This is the result of the obligation females have of taking care of the immobile pups for the duration of their haulout.

## CHAPTER 5

### THE INFLUENCE OF AGE AND SEX ON THE PATTERN AND FREQUENCY OF LOCAL MOVEMENTS DURING DIFFERENT HAULOUTS

#### 5.1 Introduction

The interactions between sex, age classes and haulout type were found to be significant in Chapter 4. This chapter deals with further analysis to determine between which ages the interactions were significant within age classes. When comparing the ages of a particular sex during a particular haulout type, only ages of individuals that participated in that particular haulout were considered. For example, breeding males included seals age 6 and older and breeding females include seals age 3 and older. When comparing between sexes, only the ages that correspond were considered, for example animals 6 to 10+ years old for breeders. In cases where the sample size was too small, data of certain ages were pooled, e.g. breeding males in the category 10+ include ages 10 to 13.

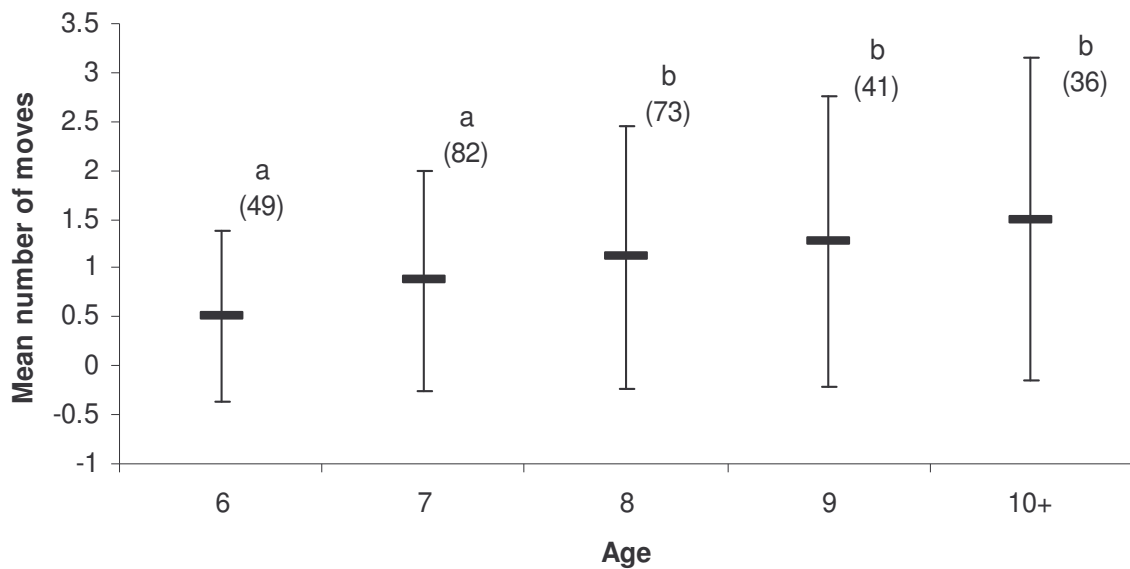
#### 5.2 Results

##### 5.2.1 Breeding males

The ANOVA (SAS, Procedure GLM) was used to determine if age had an influence on the number of times moved, number of sites visited and the distance moved by breeding male elephant seals. For the number of times moved ( $F= 4.23$ ,  $DF= 4$ ,  $P= 0.0024$  and the distance moved ( $F= 3.06$ ,  $DF= 4$ ,  $P= 0.0171$ ) the interaction was significant, but not for the number of sites visited ( $F= 2.28$ ,  $DF= 4$ ,  $P= 0.0605$ ).

***Number of times moved***

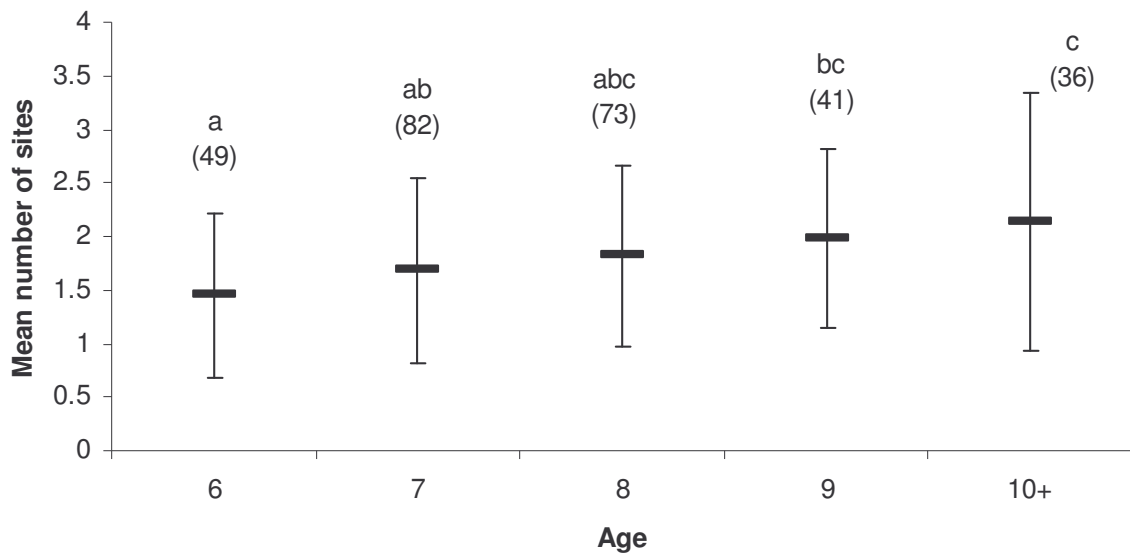
Breeding males showed a clear pattern in number of times moved during the breeding haulout. The number of times moved increased with age (Figure 5.1). Male elephant seals aged 10+ years on average moved more frequently (1.5 times) than all other ages, but this was only significant when compared to the 6 (0.51 times) and 7 (0.87 times) year olds. While the 6-year-olds on average moved less than all other ages, this was significant when compared to the 8 (1.11 times), 9 (1.27 times) and 10+ year old seals.



**Figure 5.1** Mean number of times moved by southern elephant seal breeding males of different ages at Marion Island. Means with common character (a, b) do not differ significantly. Numbers in closed brackets are sample sizes.

**Number of sites visited**

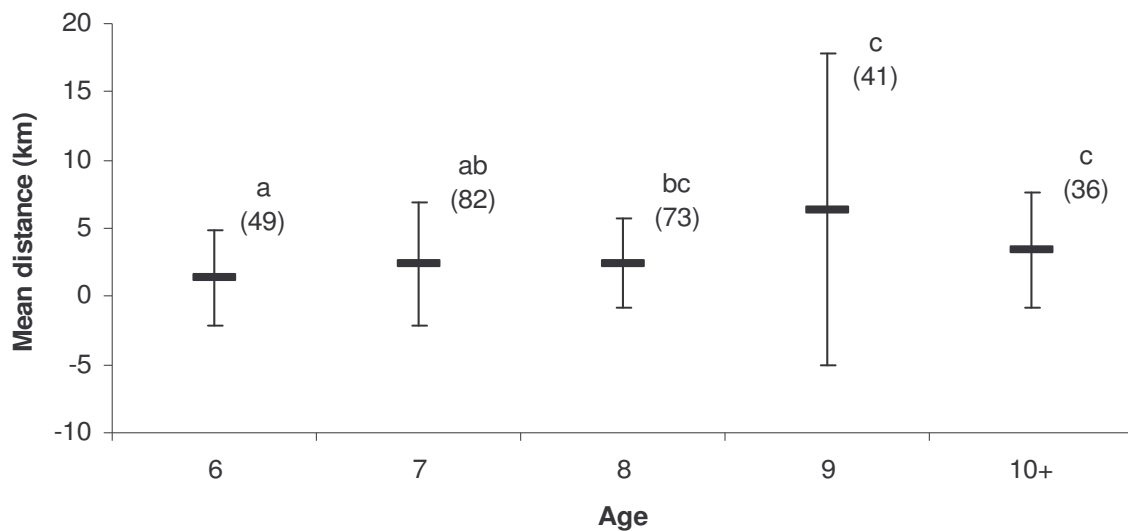
There was a clear pattern in number of sites visited by breeding males during the breeding haulout. The number of sites visited increased with age (Figure 5.2). Breeding males aged 10+ visited more sites (2.14) on average than all other ages, but this was only significant when compared to the 6 (1.45) and 7 (1.68) year olds. The 9-year-olds visited significantly more sites (1.98) than the 6-year-olds.



**Figure 5.2** Mean number of sites visited by breeding male southern elephant seals of different ages at Marion Island. Means with common character (a, b, c) do not differ significantly. Numbers in closed brackets are sample sizes.

*Distance moved*

There was a clear pattern in distance moved by breeding males during the breeding haulout. On average the 9-year-olds moved over longer (6.38 km) distances than all other males, but this was only significant when compared to the 6 (1.37 km) and 7 (2.35 km) year olds (Figure 5.3). The 6-year-olds moved over shorter distances than all other ages, but this was only significant when compared to the 8 (2.41 km), 9 (6.38) and 10+ (3.4 km) age groups. The 7-year-olds moved significantly shorter distances than the 10+ years old.



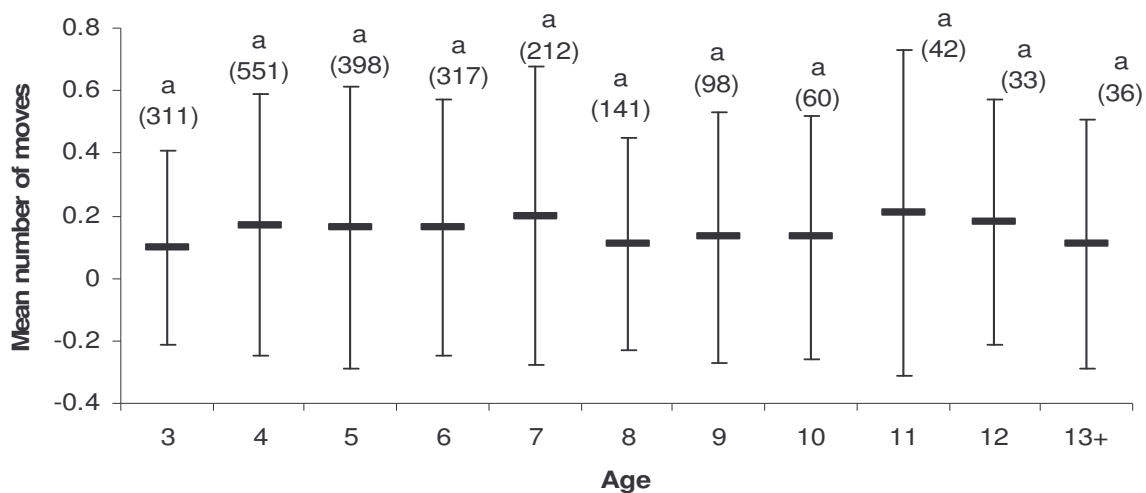
**Figure 5.3** Mean distances travelled by breeding male elephant seals of different ages at Marion Island. Means with common character (a, b, c) do not differ significantly. Numbers in closed brackets are sample sizes.

### 5.2.2 Breeding females

The ANOVA (SAS, Procedure GLM) was used to determine if age had an influence on the number of times moved, number of sites visited and the distance moved by breeding female elephant seals. For the number of times moved ( $F= 0.76$ ,  $DF= 10$ ,  $P= 0.6633$ ), the number of sites visited ( $F= 0.68$ ,  $DF= 10$ ,  $P= 0.7424$ ) and the distance moved ( $F= 0.79$ ,  $DF= 10$ ,  $P= 0.6368$ ) the interactions were not significant.

#### *Number of times moved*

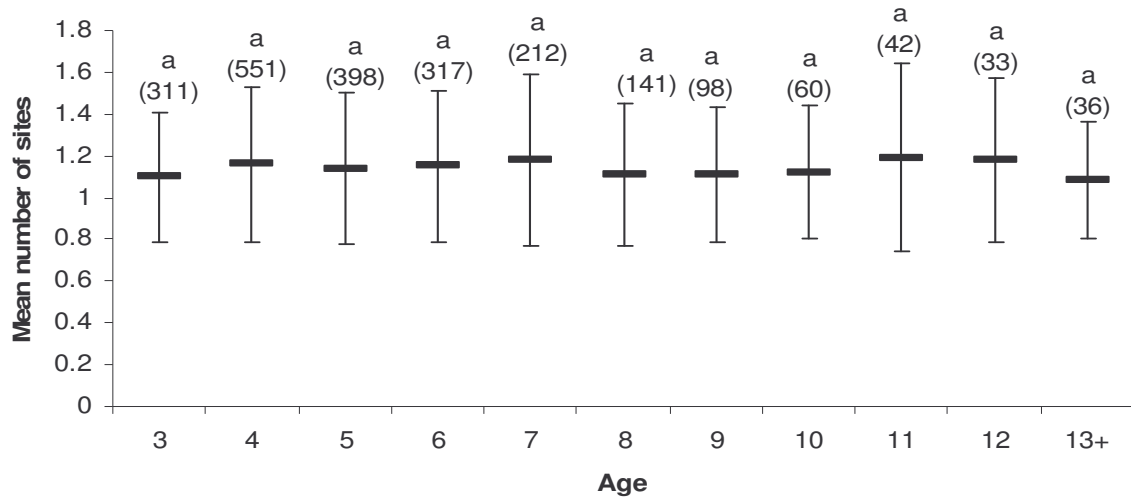
There was a clear pattern in number of times moved by females during the breeding haulout. On average, the 11-year-olds moved the most (0.21 times) but there were no significant differences amongst the age groups (Figure 5.4).



**Figure 5.4** Mean number of times moved by breeding female elephant seals of different ages at Marion Island. Means with common character (a) do not differ significantly. Numbers in closed brackets are sample sizes.

*Number of sites visited*

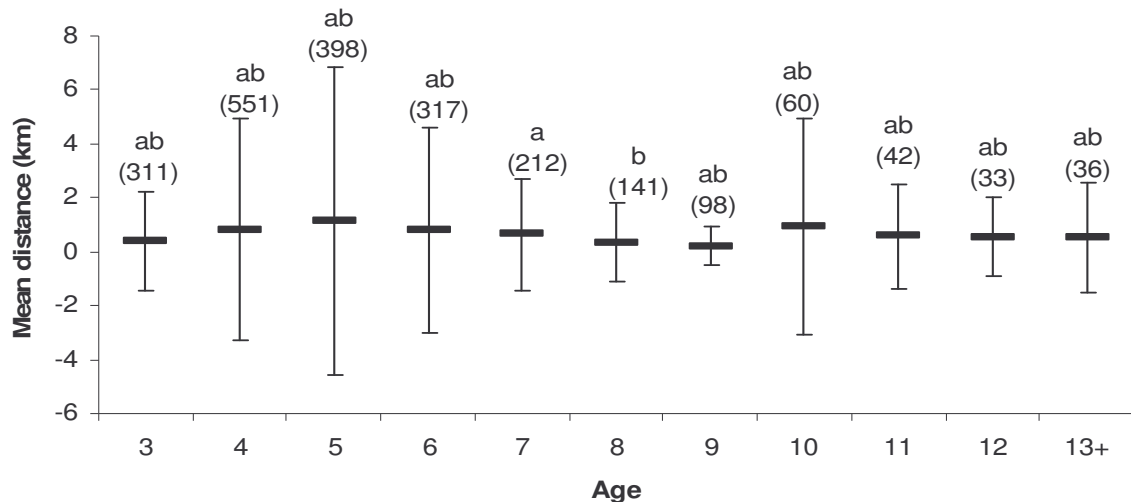
There was a clear pattern in number of sites visited by adult females during the breeding haulout. Females visited on average less than 1.20 sites during a haulout. The results showed no difference between age groups (Figure 5.5).



**Figure 5.5** Mean number of sites visited by breeding female elephant seals of different ages at Marion Island. Means with common character (a) do not differ significantly. Numbers in closed brackets are sample sizes.

*Distance moved*

There was clear pattern in distance moved by adult females during the breeding haulout. On average, breeding female moved less than 1.14 km during a haulout. Only the 7-year-olds moved significantly further (0.63 km) than the 8 (0.34 km) year old females (Figure 5.6).



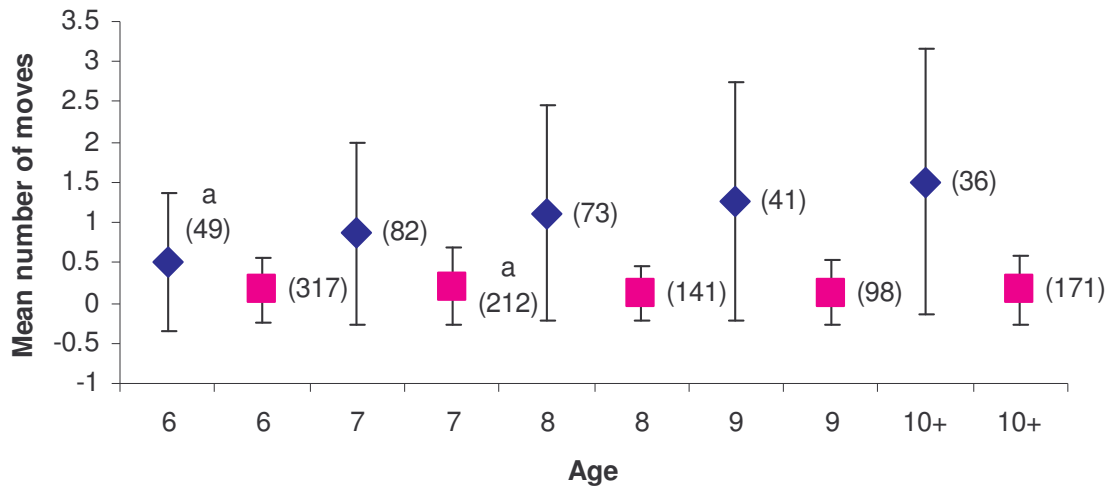
**Figure 5.6** Mean distances travelled by breeding female elephant seals of different ages at Marion Island. Means with common character (a, b) do not differ significantly. Numbers in brackets are sample sizes.

### 5.2.3 Breeding males and females

The ANOVA (SAS, Procedure GLM) was used to determine if age and sex have an influence on the number of times moved, number of sites visited and the distance moved by breeding elephant seals. For the number of times moved ( $F= 5.31$ ,  $DF= 4$ ,  $P= 0.0003$ ), the number of sites visited ( $F= 6.78$ ,  $DF= 4$ ,  $P<0.0001$ ) and the distance moved ( $F= 3.89$ ,  $DF= 4$ ,  $P= 0.0038$ ) the interactions were significant.

#### *Number of times moved*

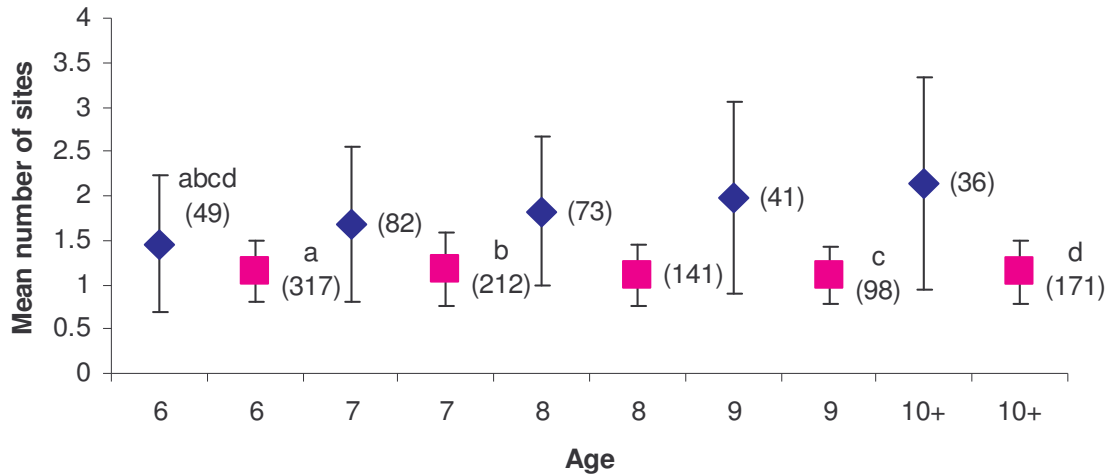
Both breeding males and females showed a clear pattern in number of times moved. The number of times moved increased with age in males. On average male  $\geq 7$ -year-olds moved significantly more (7 = 0.87 times, 8 = 1.11 times, 9 = 1.27 times, 10+ = 1.5 times) than females of all ages used in the comparison (6 = 0.16 times, 7 = 0.2 times, 8 = 0.11 times, 9 = 0.13 times, 10+ = 0.16 times). The 6-year old males on average moved significantly more (0.51 times) than females of all the ages except the 7-year-olds (Figure 5.7).



**Figure 5.7** Mean number of times moved by breeding male (◆) and female (■) elephant seals of different ages at Marion Island. Means with common character (a) do not differ significantly. Numbers in closed brackets are sample sizes.

#### *Number of sites visited*

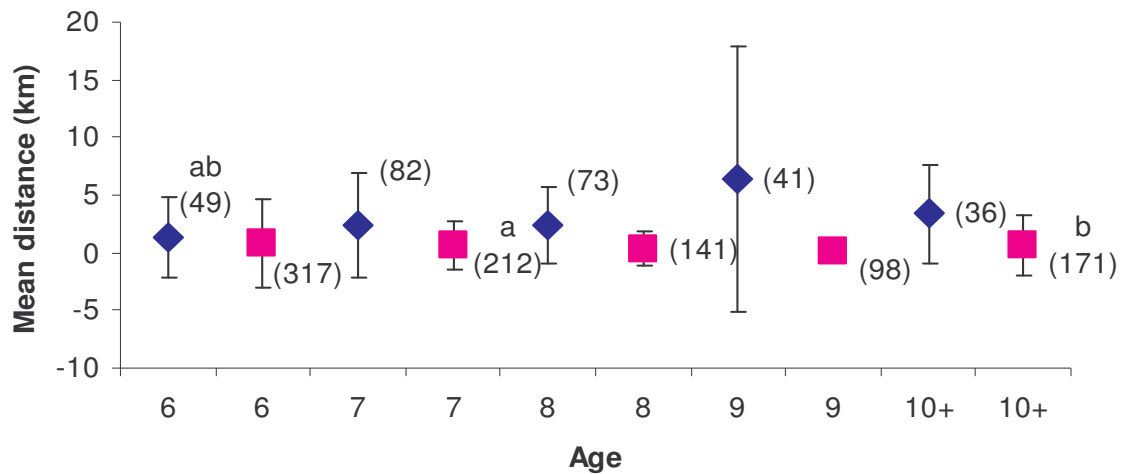
Both breeding male and female elephant seals showed a different pattern in the number of sites visited during the breeding haulout. There was an increase in the number of sites visited with an increase in age by males (Figure 5.8). Breeding males  $\geq 7$  years old significantly visited more (7 = 1.68, 8 = 1.82, 9 = 1.92, 10+ = 2.14) sites than females of all the ages used in the comparison (6 = 1.15, 7 = 1.18, 8 = 1.11, 9 = 1.11, 10+ = 1.44). The 6-year old males only visited significantly more (1.45) sites than the 8-year old breeding females.



**Figure 5.8** Mean number of sites visited by breeding male (◆) and female (■) elephant seals of different ages at Marion Island. Means with common character (a, b, c, d) do not differ significantly. Numbers in closed brackets are sample sizes.

#### *Distance moved*

Both breeding male and female elephant seals showed a different pattern in distance moved during the breeding haulout. The distance covered by females decreased with an increase in age (Figure 5.9). Southern elephant seal males  $\geq 7$  years old on average moved significantly further (7 = 2.35 km, 8 = 2.41 km, 9 = 6.38 km, 10+ = 3.4) than females of all comparable ages (6 = 0.8 km, 7 = 0.63 km, 8 = 0.34 km, 9 = 0.2 km, 10+ = 0.68). The 6-year old males moved on average significantly further (1.37 km) than females of 6, 8 and 9 years old but not further than females aged 7 and 10+ years.



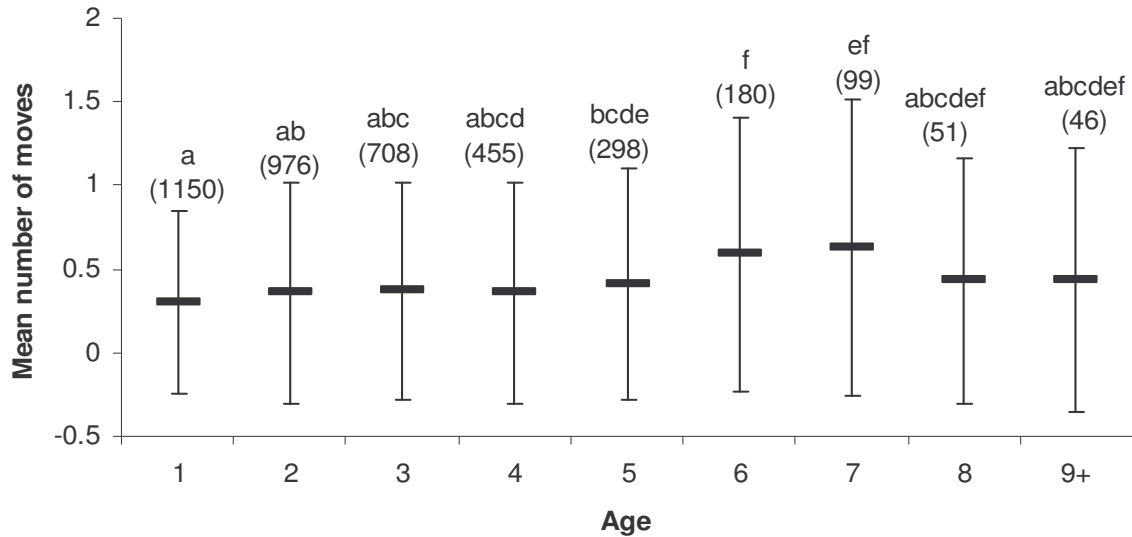
**Figure 5.9** Mean distances travelled by breeding male (♦) and female (■) elephant seals of different ages at Marion Island. Means with common character (a, b) do not differ significantly. Numbers in closed brackets are sample sizes.

#### 5.2.4 Moulting males

The ANOVA (SAS, Procedure GLM) was used to determine if age have an influence in the number of times moved, number of sites visited and the distance moved by moulting male southern elephant seals at Marion Island. For the number of times moved ( $F= 3.99$ ,  $DF= 8$ ,  $P= 0.0001$ ) and the number of sites visited ( $F= 2.74$ ,  $DF= 8$ ,  $P= 0.0051$ ) the interaction was significant, but not for the distance moved ( $F= 1.73$ ,  $DF= 8$ ,  $P= 0.0873$ ).

##### *Number of times moved*

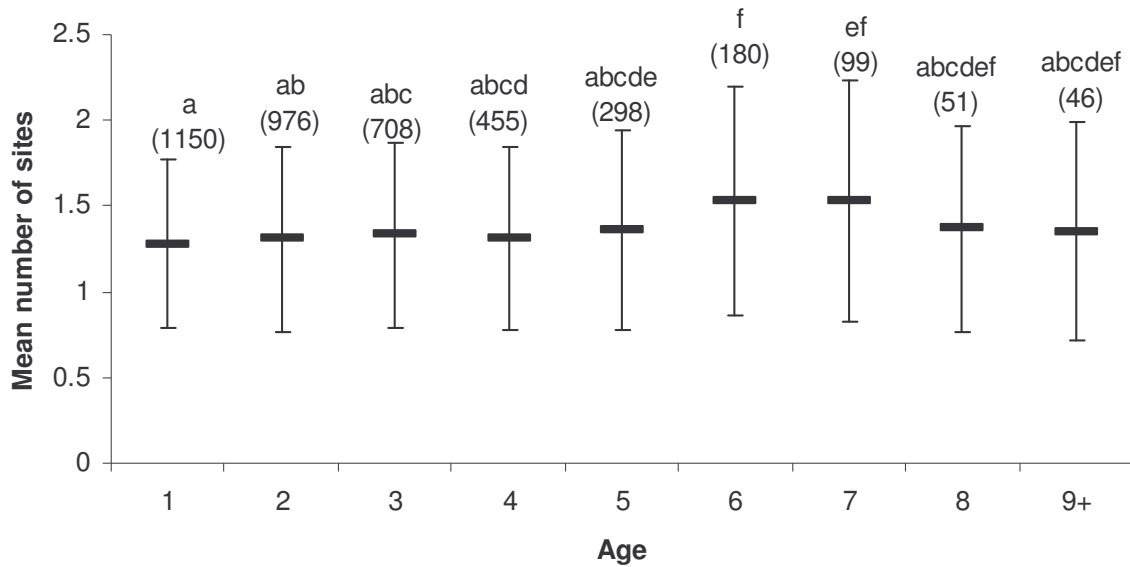
Elephant seal males during the moult haulout showed no clear pattern in number of times moved during a haulout. The moulting males moved on average less than 0.63 times during a haulout. The 7-year-olds moved more (0.63 times) than all other males of the different ages, but this was only significant when compared to the 1- (0.3 times), 2- (0.36 times), 3- (0.37 times), and 4-year-olds (0.36 times). Also the 6-year-olds moved on average significantly more than the males aged 1 to 5 years (Figure 5.10).



**Figure 5.10** Mean number of times moved by elephant seal males of different ages during the moult haulout at Marion Island. Means with common character (a, b, c, d, e, f) do not differ significantly. Numbers in closed brackets are sample sizes.

#### *Number of sites visited*

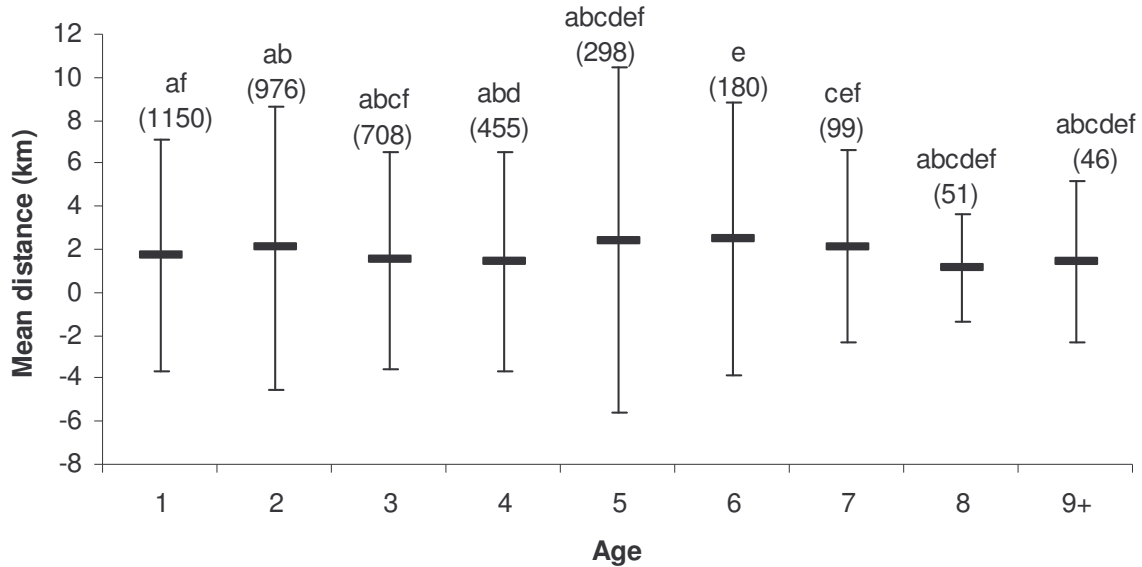
Moulting elephant seal males showed no clear pattern in number of sites visited during a haulout. The moulting males visited on average less than 1.53 sites during a haulout (Figure 5.11). The 6-year old males visited more (1.53) sites than all the other males, but this was only significant when compared to the 1- (1.28), 2- (1.31), 3- (1.33), 4- (1.31) and 5-year-olds (1.36). The 7-year-olds also visited significantly more (1.53) sites than the males aged 1 to 4 years old.



**Figure 5.11** Mean number of sites visited by elephant seal males of different ages during the moult haulout at Marion Island. Means with common character (a, b, c, d, e, f) do not differ significantly. Numbers in closed brackets are sample sizes.

#### *Distance moved*

There was no clear pattern in the distances moved by male elephant seals during the moult haulout. Males moved on average less than 2.45 km during the haulout (Figure 5.12). On average the 6-year-olds moved a greater distance (2.45 km) than males of other ages, but this was only significant when compared to the 1- (1.71 km), 2- (2.06 km), 3- (1.49 km) and 4- (1.43 km) year old males. The 7-year-olds also moved significantly further (2.13 km) than the 2- and 4-year-olds.



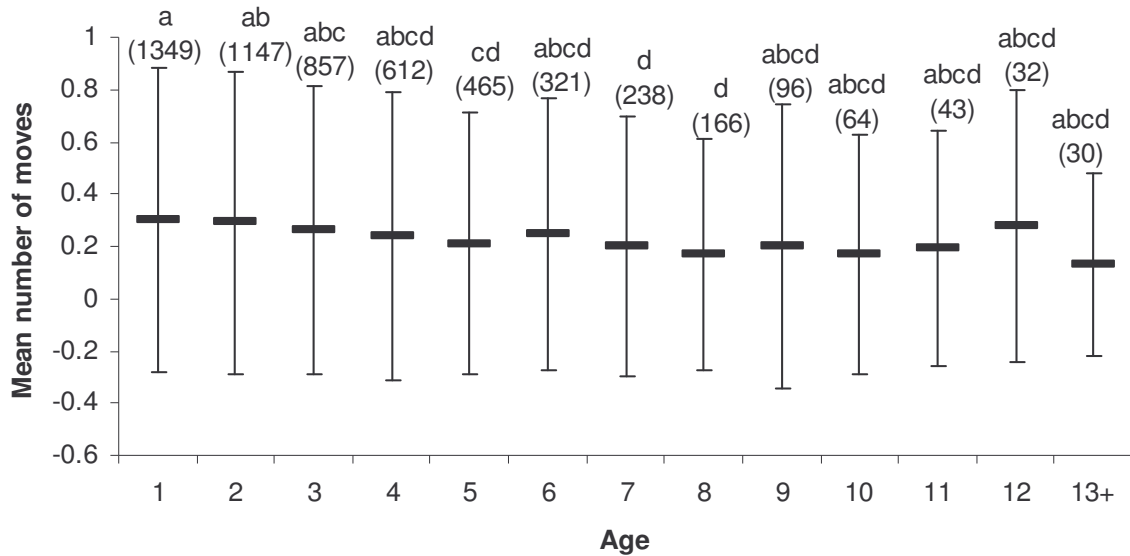
**Figure 5.12** Mean distances travelled by elephant seal males of different ages during the moult haulout at Marion Island. Means with common character (a, b, c, d, e, f) do not differ significantly. Numbers in closed brackets are sample sizes.

### 5.2.5 Moulting females

The ANOVA (SAS, Procedure GLM) was used to determine if age have an influence on the number of times moved, number of sites visited and the distance moved by moulting female elephant seals. For the number of times moved ( $F= 1.75$ ,  $DF= 12$ ,  $P= 0.0509$ ), the number of sites visited ( $F= 1.81$ ,  $DF= 12$ ,  $P= 0.0409$ ) and the distance moved ( $F= 2.35$ ,  $DF= 12$ ,  $P= 0.0053$ ) the interactions were significant.

#### *Number of times moved*

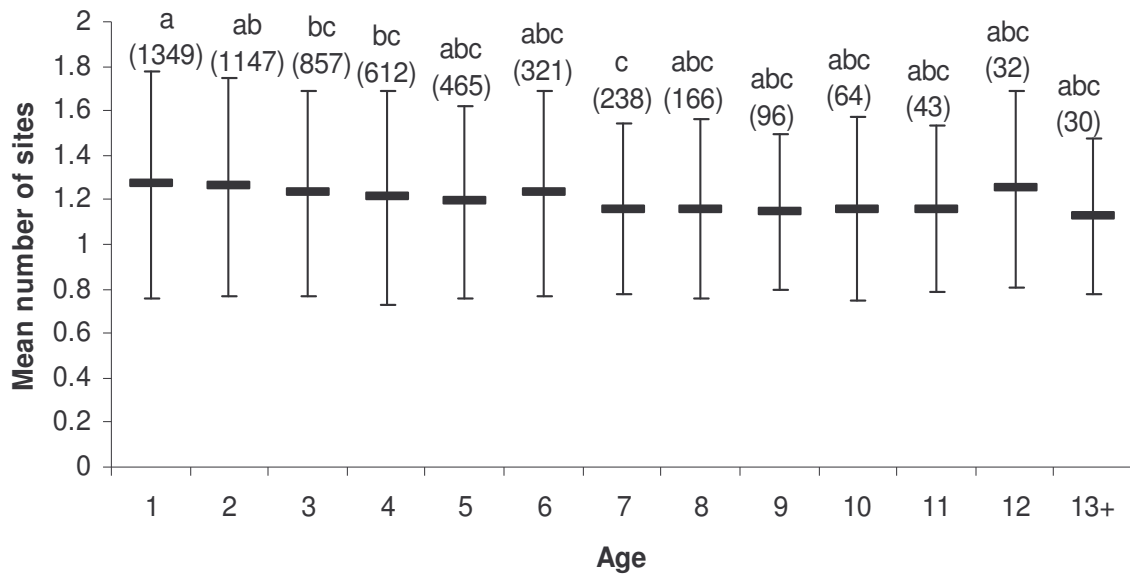
There was no clear pattern for female elephant seals in the number of times moved during the moult haulout. At Marion Island females on average moved less than 0.3 times during the moult haulout (Figure 5.13). Female 1-year-olds moved more (0.3 times) than all other females, but this was only significant when compared to the 5- (0.21 times), 7- (0.2 times) and 8-year-olds (0.17 times). The 2-year old females also moved significantly more (0.29 times) than the 5- and 8-year-olds. The 3-year-olds also moved significantly more (0.26 times) than the 8-year-olds.



**Figure 5.13** Mean number of times moved by female elephant seals of different ages during the moult haulout at Marion Island. Means with common character (a, b, c, d) do not differ significantly. Numbers in closed brackets are sample sizes.

#### *Number of sites visited*

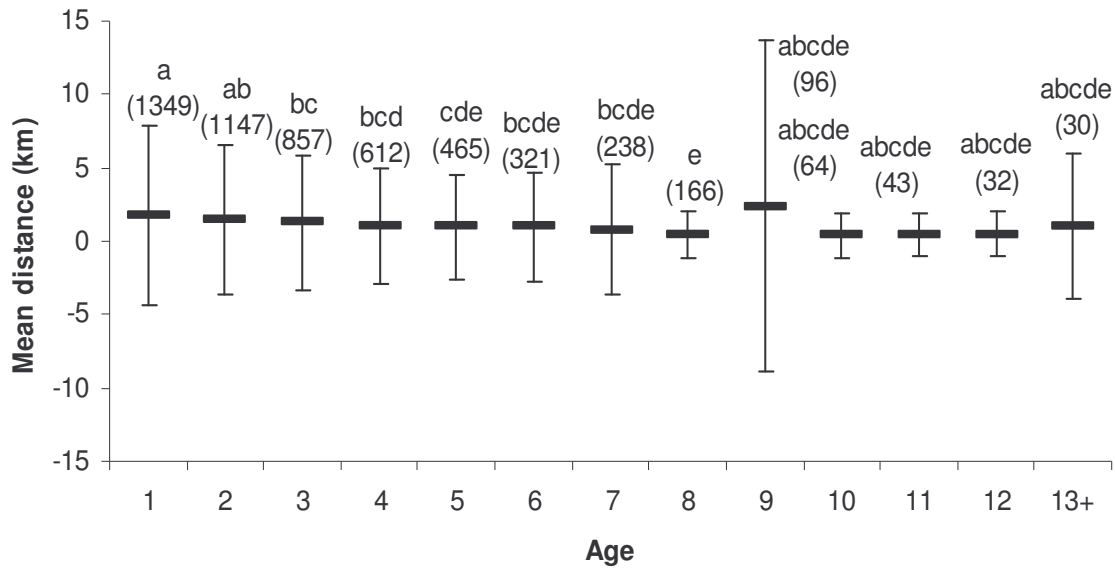
Females showed no clear pattern in the number of sites visited during the moult haulout. Females visited on average less than 1.27 sites during a haulout (Figure 5.14). The 1-year old females on average visited more sites (1.27) than all other females, but this was only significant when compared to the 3- (1.23), 4- (1.21) and 7-year-olds (1.16). The 2-year-olds also visited significantly fewer sites (1.26) than the 7-year-olds.



**Figure 5.14** Mean number of sites visited by female elephant seals of different ages during the moult haulout at Marion Island. Means with common character (a, b, c) do not differ significantly. Numbers in closed brackets are sample sizes.

#### *Distance moved*

The females showed no clear pattern in the distance moved during the moult haulout. On average, the females moved less than 2.37 km during a haulout (Figure 5.15). Moulting females aged 1 to 4 years on average moved significantly further (1 = 1.77 km, 2 = 1.42 km, 3 = 1.27 km, 4 = 1.01 km) than the 8-year-olds (0.43 km). The 1-year-olds also moved significantly further than the 3 to 7 years old females (5 = 0.96 km, 6 = 0.98 km, 7 = 0.78 km), and the 2-year-olds moved significantly further than the 5- and 8-year-olds.



**Figure 5.15** Mean distances travelled by female elephant seals of different ages during the moult haulout at Marion Island. Means with common character (a, b, c, d, e) do not differ significantly. Numbers in closed brackets are sample sizes.

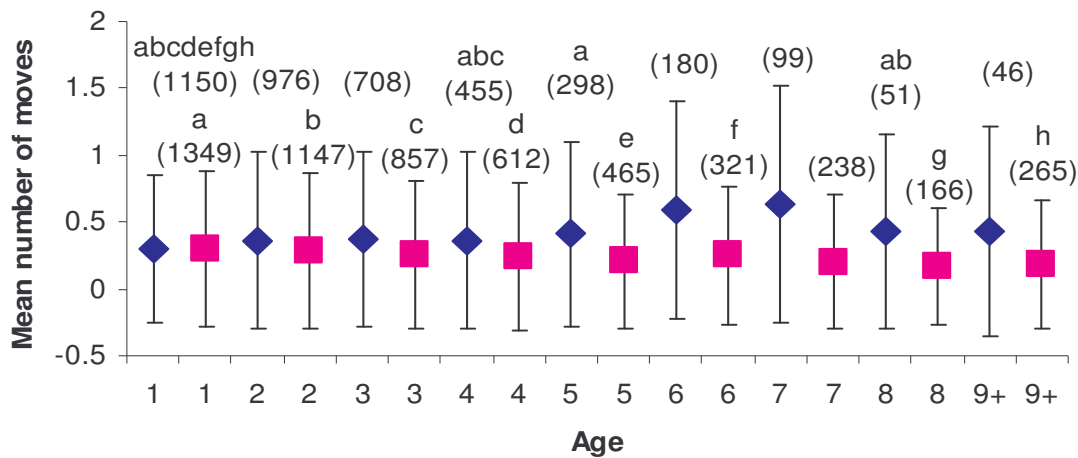
### 5.2.6 Moulting males and females

The ANOVA (SAS, Procedure GLM) was used to determine if age and sex have an influence on the number of times moved, number of sites visited and the distance moved by moulting male and female elephant seals. The results showed that for the number of times moved ( $F= 5.76$ ,  $DF= 8$ ,  $P< 0.0001$ ), the number of sites visited ( $F= 4.43$ ,  $DF= 8$ ,  $P<0.0001$ ) and the distance moved ( $F= 3.50$ ,  $DF= 8$ ,  $P= 0.0005$ ) the interactions were significant.

#### *Number of times moved*

Moulting female elephant seals, as they aged, showed a clear pattern throughout in the number of sites visited during the moult haulout as compared to moulting males, which followed a pattern only until age five (Figure 5.16). Male and female elephant seals on average moved less than 0.63 times and 0.3 times respectively during the moult haulout. All moulting male elephant seals moved significantly more than moulting females of the same ages, except the 1-year-olds ( $m= 0.3$  times,  $f= 0.3$  times). The 1-year old males moved more than all females, but this was only significant when compared to the 7-year old (0.2 times) females. The 4-year old males moved significantly

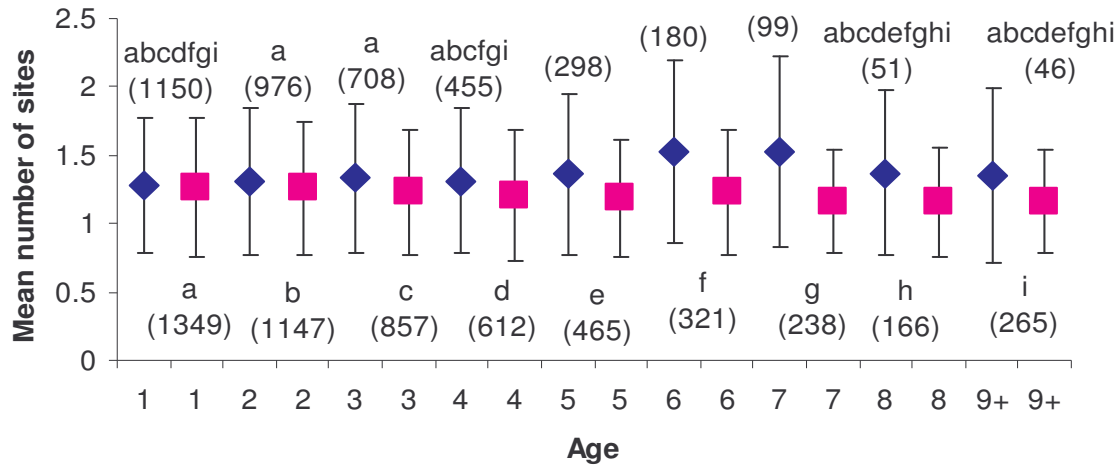
more (0.36 times) than all females, except the 1-(0.3 times), 2-(0.29 times) and 3-year old (0.26 times) females. The 5-year old males moved significantly more (0.41 times) than all females, except the 1-year-olds. In addition, the 8-year old males moved significantly more (0.43 times) than females of all different ages except the 1-and 2-year old females.



**Figure 5.16** Mean number of times moved by male (♦) and female (■) elephant seals of different ages during the moult haulout at Marion Island. Means with common character (a, b, c, d, e, f, g, h) do not differ significantly. Numbers in closed brackets are sample sizes.

### *Number of sites visited*

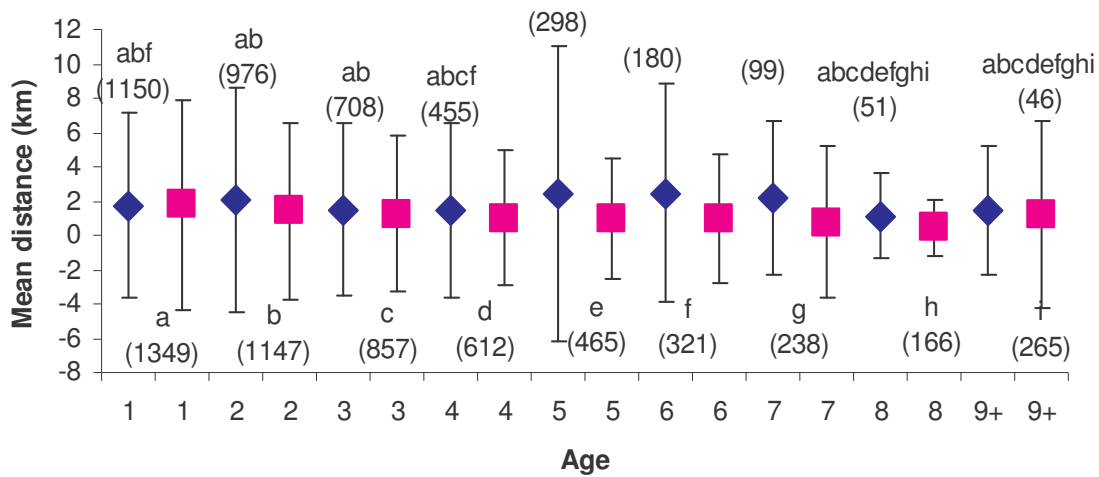
There was clear pattern by female elephant seals as they aged in the number of sites visited during the moult haulout as compared to males, which followed a pattern until age five (Figure 5.17). On average male and female elephant seals visited less than 1.53 and 1.27 sites respectively during the moult haulout. The 9+ years old females visited fewer sites (1.16) than males of all ages, but this was only significant when compared to the 5- (1.36), 6- (1.53), and 7-year old (1.53) males. The 1-year old males visited more sites (1.28) than females of all ages, but this was only significant when compared to the 5- (1.19) and 8-year old (1.16) females. The 4-year old males visited more sites (1.31) than females of all ages, but this was only significant when compared to the 5- and 8-year old females. The 2- and 3-year old males visited significantly more sites than females of all ages except the 1-year old females. All moulting males of different ages visited significantly more sites than females of the same ages, except the 1-, 8- and 9-year-olds.



**Figure 5.17** Mean number of sites visited by male (♦) and female (■) elephant seals of different ages during the moult haulout at Marion Island. Means with common character (a, b, c, d, e, f, g, h, i) do not differ significantly. Numbers in closed brackets are sample sizes.

### *Distance moved*

There was a clear pattern by female elephant seals throughout their ages in the distance moved during the moult haulout as compared to males, which follow a pattern only until age five (Figure 5.18). Male and female elephant seals on average moved distances of less than 2.45 km and 1.77 km respectively during the moult haulout. All moulting males moved significantly further than moulting females of the same ages, except for the 1- (m=1.71, f=1.77), 2- (m=2.06, f=1.42), 8- (m=1.11 km, f= 0.43 km) and 9+ (m=1.4, f=1.19) -year-olds. Although the results were not significant, the 1-year old females moved further (1.77 km) than male 1- (1.71 km), 3- (1.49 km), 4- (1.43 km), 8- (1.11 km) and 9+ (1.4 km) -year-olds. Except for the 1-year old females, the 1-year old males moved further than females of all the ages, but this was not significant when compared to the 2- (1.42 km) and 6- (0.98 km)-year old females. The 2- and 3-year old males moved further than females of all the ages, but this was not significant when compared to the 1- and 2-year old females. The 4-year old males moved further than females of all the ages, but this was only significant when compared to the 5- (0.96 km), 7- (0.78 km), 8- (0.43 km) and 9+ -year old (0.27) females.



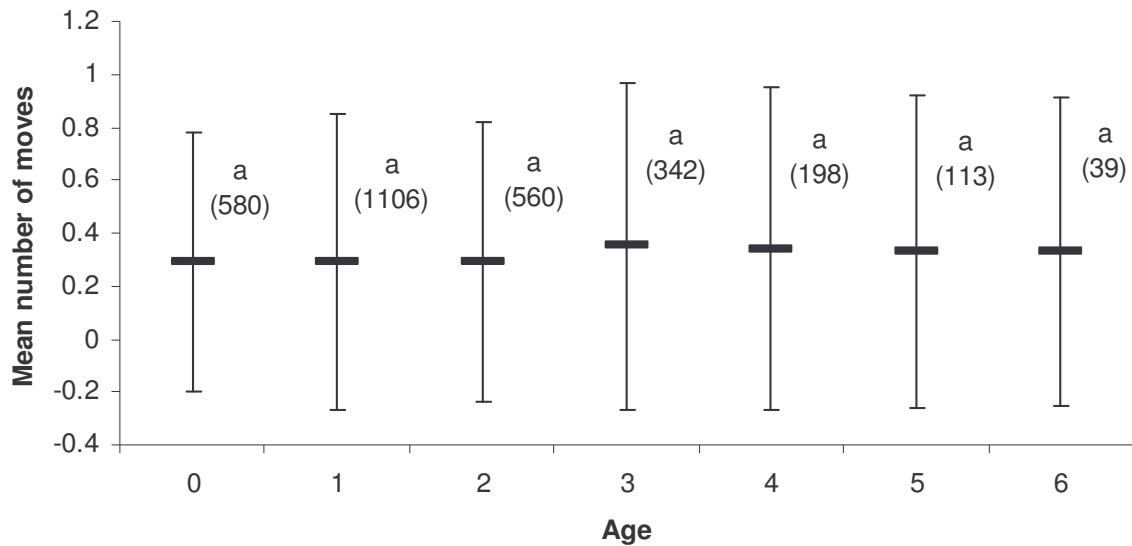
**Figure 5.18** Mean distances travelled by male (♦) and female (■) elephant seals of different ages during the moult haulout at Marion Island. Means with common character (a, b, c, d, e, f, g, h, i) do not differ significantly. Numbers in closed brackets are sample sizes.

### 5.2.7 Wintering males

The ANOVA (SAS, Procedure GLM) was used to determine if age had an influence on the number of times moved, number of sites visited and the distance moved by wintering male elephant seals. For the number of times moved ( $F= 0.92$ ,  $DF= 6$ ,  $P= 0.4817$ ), the number of sites visited ( $F= 0.34$ ,  $DF= 6$ ,  $P= 0.9141$ ) and the distance moved ( $F= 0.83$ ,  $DF= 6$ ,  $P= 0.5490$ ) the interactions were not significant.

#### *Number of times moved*

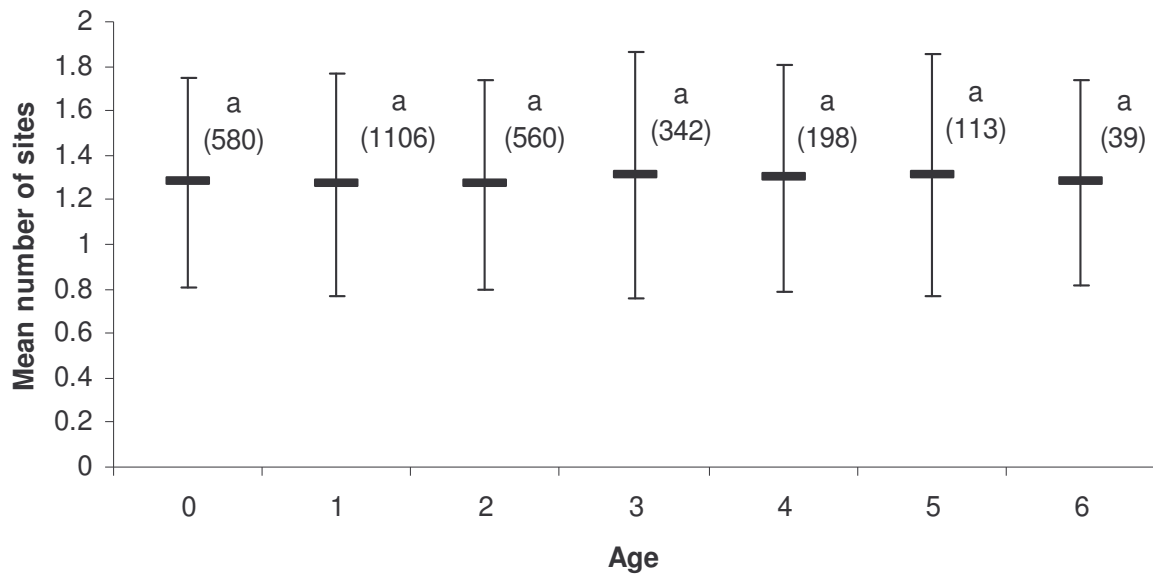
Wintering male elephant seals showed no clear pattern in the number of times moved during the winter haulout. On average, males hauling out for the winter moved less than 0.35 times during that haulout (Figure 5.19). Although the male 3-year-olds moved more (0.35 times) than other males of all ages (0 = 0.29 times, 1 = 0.29 times, 2 = 0.29 times, 4 = 0.34 times, 5 = 0.33 times, 6 = 0.33 times), these results showed no significant difference amongst the age groups.



**Figure 5.19** Mean number of times moved by male elephant seals of different ages during the winter haulout at Marion Island. Means with common character (a) do not differ significantly. Numbers in closed brackets are sample size.

#### *Number of sites visited*

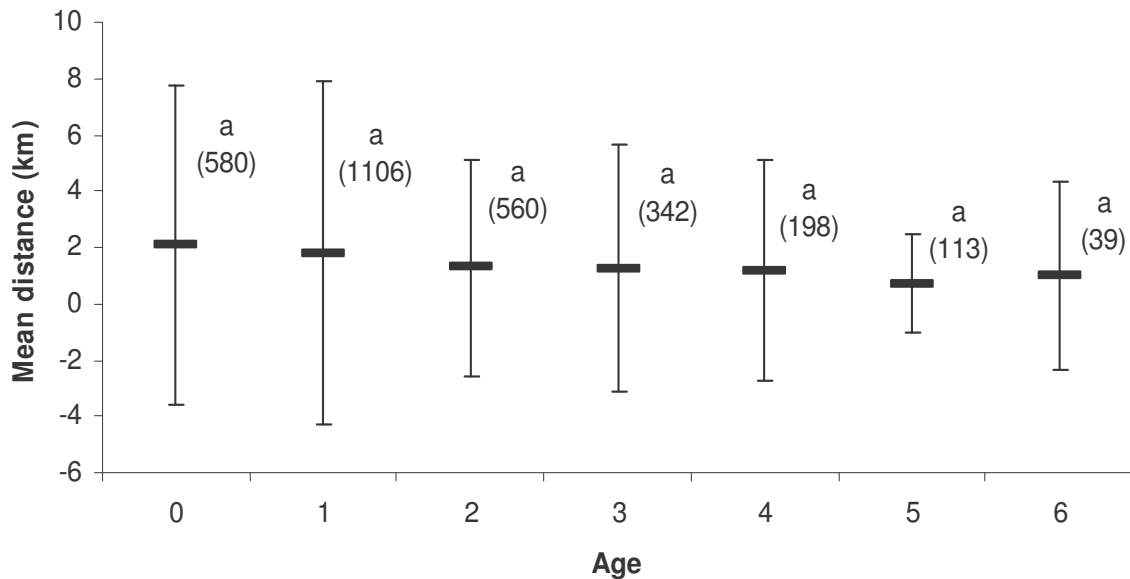
Male elephant seals showed no clear pattern in the number of sites visited during the winter haulout. Wintering male elephant seals on average visited less than 1.31 sites during the winter haulout (Figure 5.20). Although the 3-(1.31 times) and 5-(1.31 times)-year-olds visited more sites than other males of all the ages (0 = 1.28 times, 1 = 1.27 times, 2 = 1.27 times, 4 = 1.3 times, 6 = 1.28 times), the results were not significant.



**Figure 5.20** Mean number of sites visited by male elephant seals of different ages during the winter haulout at Marion Island. Means with common character (a) do not differ significantly. Numbers in closed brackets are sample size.

#### *Distance moved*

Male elephant seals showed no clear pattern in the distance moved during the winter haulout, when they moved, on average, less than 2.09 km (Figure 5.21). Underyearling male elephant seals moved longer distances (2.09 km) than other males of all ages (1 = 1.79 km, 2 = 1.27 km, 3 = 1.23 km, 4 = 1.17 km, 5 = 0.71 km & 6 = 1 km), but these results were not significant.



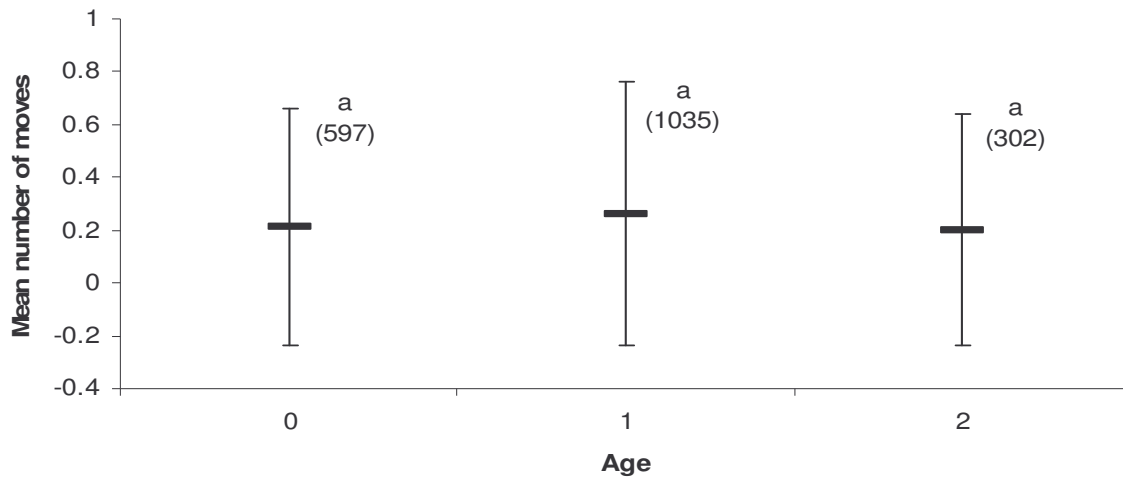
**Figure 5.21** Mean distances travelled by male elephant seals of different ages during the winter haulout at Marion Island. Means with common character (a) do not differ significantly.

### 5.2.8 Wintering Females

The ANOVA (SAS, Procedure GLM) was used to determine if age had an influence on the number of times moved, number of sites visited and the distance moved by wintering female elephant seals. For the number of times moved ( $F= 0.09$ ,  $DF= 2$ ,  $P= 0.9117$ ), the number of sites visited ( $F= 1.35$ ,  $DF= 2$ ,  $P= 0.2582$ ) and the distance moved ( $F= 1.74$ ,  $DF= 2$ ,  $P= 0.1758$ ) the interactions were not significant.

#### *Number of times moved*

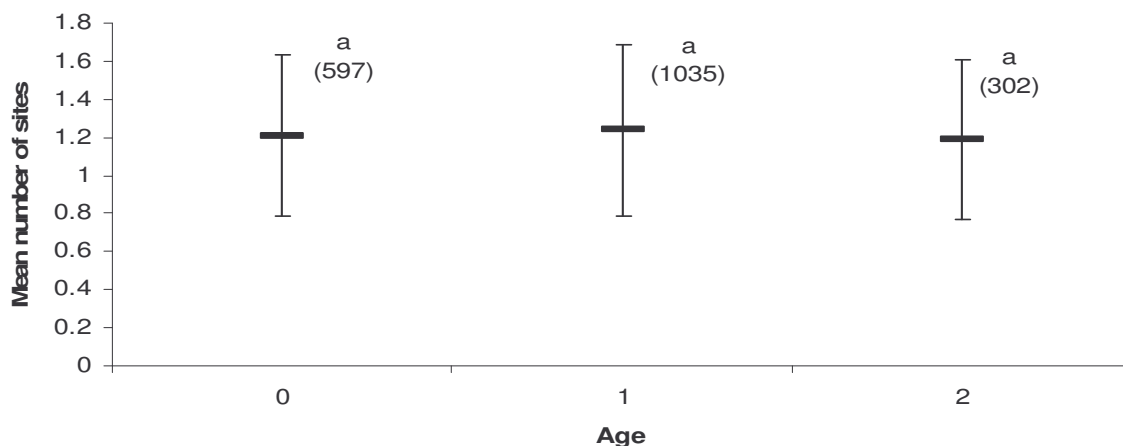
Female elephant seals showed no clear pattern in the number of times moved during the winter haulout. On average, wintering female elephant seals moved less than 0.26 times during the winter haulout (Figure 5. 22). The 1-year-olds moved more (0.26 times) than the underyearling (0.21 times) and 2-year old (0.2 times) females, but these results were not significant.



**Figure 5.22** Mean number of times moved by female elephant seals of different ages during the winter haulout at Marion Island. Means with common character (a) do not differ significantly. Numbers in closed brackets are sample size.

#### *Number of sites visited*

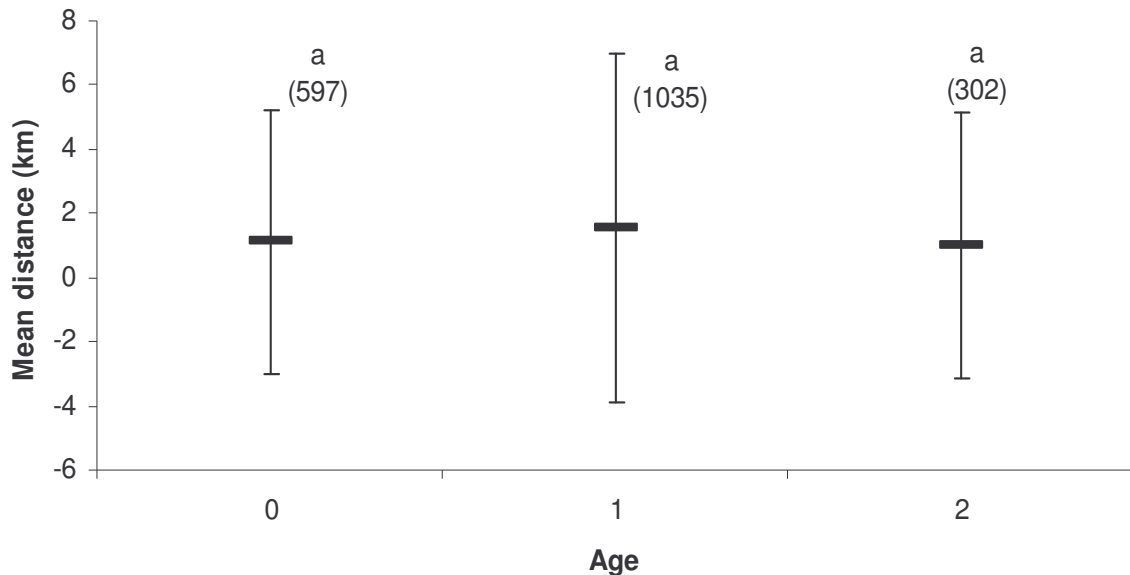
Female elephant seals showed no clear pattern in the number of sites visited during the winter haulout. On average, wintering females visited less than 1.24 sites during a haulout (Figure 5.23). The 1-year old females visited more (1.24) sites than the underyearling (1.21) and 2-(1.19)-year-olds, but these results were not significant.



**Figure 5.23** Mean number of sites visited by female elephant seals of different ages during the winter haulout at Marion Island. Means with common character (a) do not differ significantly. Numbers in closed brackets are sample size.

***Distance moved***

The female elephant seals showed no clear pattern in the distance moved during the winter. On average wintering female elephant seals moved less than 1.54 km during the winter haulout (Figure 5.24). The 1-year-olds moved further (1.54 km) than the underyearling (1.13 km) and 2- (1.02 km) year old females, but these results were not significant.



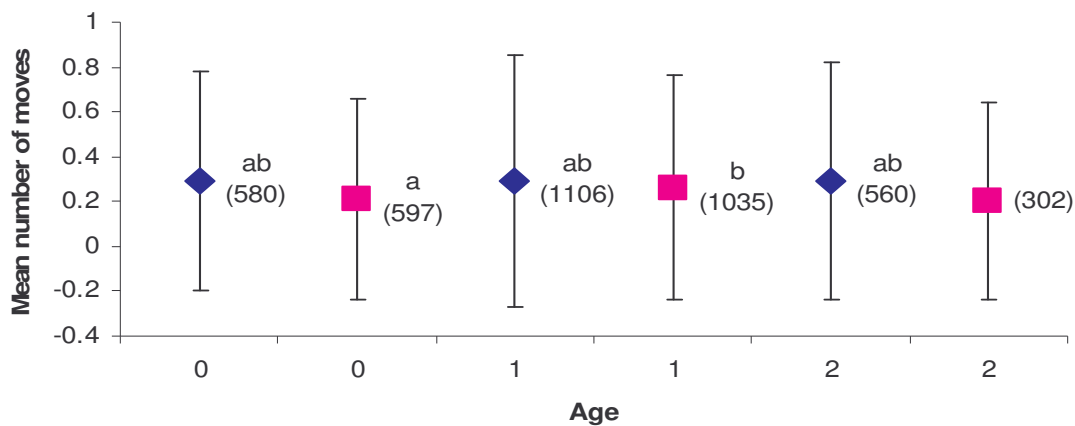
**Figure 5.24** Mean distances travelled by female elephant seals of different ages during the winter haulout at Marion Island. Means with common character (a) do not differ significantly. Numbers in closed brackets are sample size.

**5.2.9 Wintering males and females**

The ANOVA (SAS, Procedure GLM) was used to determine if age and sex have an influence on the number of times moved, number of sites visited and the distance moved by wintering male and female elephant seals. For the number of times moved ( $F= 5.03$ ,  $DF= 2$ ,  $P= 0.0065$ ) and the distance moved ( $F= 3.35$ ,  $DF= 2$ ,  $P=0.0351$ ) the interactions were significant, but not for the number of sites visited ( $F= 1.58$ ,  $DF= 2$ ,  $P= 0.2065$ ).

***Number of times moved***

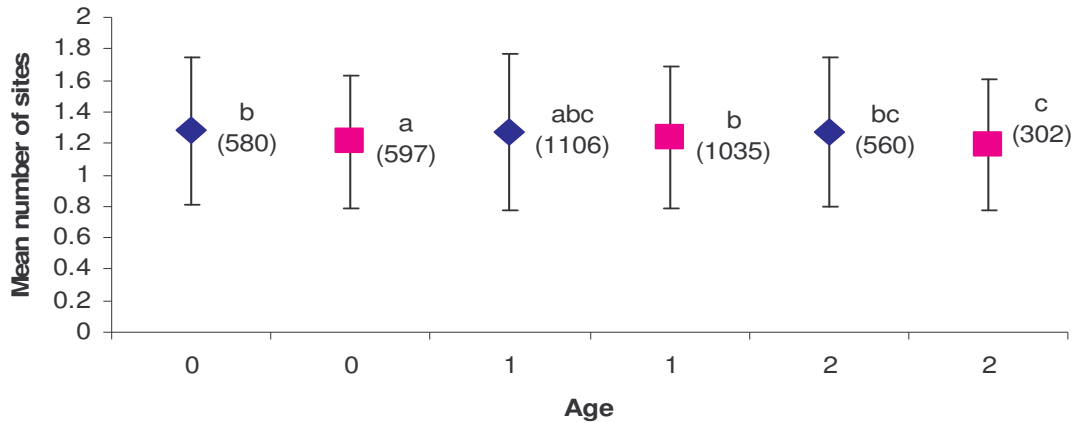
Male elephant seals showed a clear pattern in the number of times moved during the winter haulout as compared to females. Male and female elephant seals moved less than 0.29 times and 0.26 times respectively during the winter haulout (Figure 5.25). The 2-year old females on average moved significantly less (0.2 times) than males of all ages hauling out at this time (0 = 0.29 times, 1 = 0.29 times, 2 = 0.29 times). Although all the males moved more than females of the same age, this difference was only significant for 2-year-olds.



**Figure 5.25** Mean number of times moved by male (◆) and female (■) elephant seals of different ages during the winter haulout at Marion Island. Means with common character (a, b) do not differ significantly. Numbers in closed brackets are sample size.

***Number of sites visited***

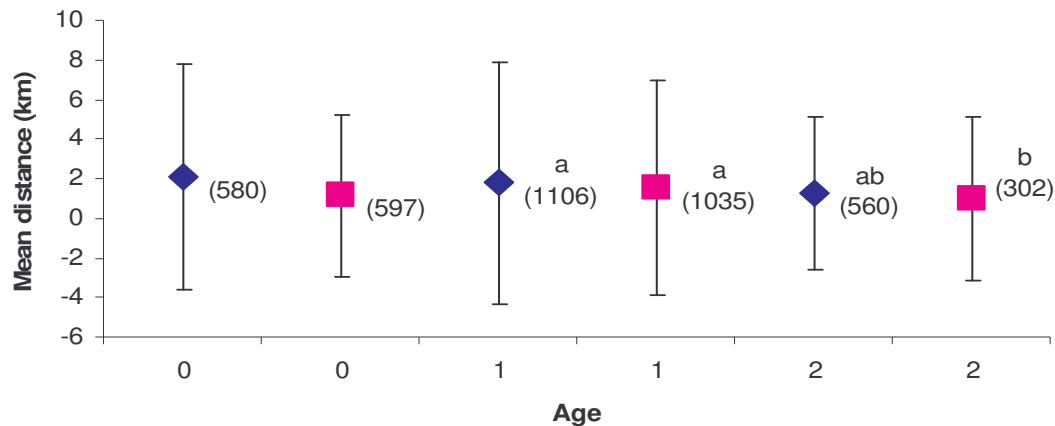
Male elephant seals showed a clear pattern in the number of sites visited during the winter haulout as compared to the females. Males and females visited less than 1.28 and 1.24 sites respectively during the winter haulout (Figure 5.26). On average, all males visited more sites than females of the same age, but this was only significant between the underyearlings ( $m = 1.28$ ,  $f = 1.21$ ). Although the results were not significant, the 1-year old males visited more sites (1.27) than all age groups of females. The 2-year old females visited fewer sites (1.19) than males of all the ages, but this was only significant when compared to underyearling males (1.28). The 2-year old males visited more sites (1.27) than all females, but this was significant only when compared to the underyearling females.



**Figure 5.26** Mean number of sites visited by male (♦) and female (■) elephant seals of different ages during the winter haulout at Marion Island. Means with common character (a, b, c) do not differ significantly. Numbers in closed brackets are sample size.

#### *Distance moved*

Male elephant seals showed a clear pattern in the distance moved during the winter haulout as compared to females. There was a decrease in the distance moved with an increase in age. On average male and female elephant seals moved distances of less than 2.09 km and 1.54 km respectively during the winter haulout (Figure 5.27). On average, all males moved further than females of the same age, but this was only significant for underyearlings (m= 2.09 km, f= 1.13 km). Underyearling males moved significantly further than females of all ages (1 = 1.54 km, 2 = 1.02 km), while underyearling females moved significantly less than males of all the ages (1 = 1.79 km, 2 = 1.27 km).



**Figure 5.27** Mean distances travelled by wintering male (♦) and female (■) elephant seals at Marion Island. Means with common character (a, b) do not differ significantly. Numbers in closed brackets are sample size.

### 5.3 Discussion

The patterns and frequencies of numbers of times moved, numbers of sites visited and distances moved by southern elephant seals of different ages and sex were measured during the winter, moult and breeding seasons. Since the needs and requirements for each haulout type and sex are different, the results for each of these categories will be discussed separately.

#### 5.3.1 Breeding males

The results showed a clear pattern in the number of times moved and number of sites visited during the breeding haulout, but not for distance moved. There was a significant difference between age classes and it was the older animals that moved more, visited more sites and moved further during the breeding haulout, owing this to their different social ranks. The younger bulls (6- and 7-year-olds) were more inexperienced breeders and therefore usually only attain the bachelor status. The older bulls were more experienced breeders and more often beachmasters, assistant beachmasters or challengers. Therefore older males were more often involved in dominance interactions in defence of their harems or for access to cows. These interactions seem to happen more readily during the early stages of the breeding season, when no, or very few, females are in estrus (McCann 1983; Carlini *et al.* 2002). At this time males move from one harem to another in

an attempt to find those with the maximum number of cows, which will offer more mating opportunities (Carlini *et al.* 2002).

Beachmaster turnover on Marion Island was possibly high, as was the case on Macquarie Island (Carrick *et al.* 1962b). On the latter island, many dominance interactions took place, most of which involved older bulls, forcing them to move around and change sites more often than the younger bulls. Furthermore, males spent significantly more time moving around and vocalizing prior to harem formation than they did after harem formation (McCann 1983). Also of importance was the duration of the breeding season haulout between the younger and older breeders. This has been shown to be longer at Macquarie for the older and stronger bulls (Carrick *et al.* 1962a). Older animals therefore had more time over which to move during the breeding season, and this was the case for Marion Island. Early arrival at the breeding site seems to be a factor which helps males to attain a high dominance rank because of their prior resident status (Haley *et al.* 1994): and a high dominance rank leads to high reproductive success (Le Boeuf & Peterson 1969, McCann 1981, Haley *et al.* 1994, Galimberti & Boitani 1999).

### **5.3.2 Breeding females**

The results showed no significant differences amongst all ages of females for all three measures, except in one case. Seven-year-olds were found to move significantly further than the 8-year-olds. While the reason for this result remains obscure, the overwhelming majority of the evidence showed that adult females of all ages act alike in terms of movement during the breeding season. These results might stem from the fact that there was far greater similarity in social ranking between adult females than adult males. Furthermore, southern elephant seals show a high degree of fidelity to their natal site, and to the site of first reproduction (Hofmeyr 2000). There is reason, however, to expect primiparous or younger cows to move more frequently, to visit more sites and to move further than multiparous cows. Observations of adult female elephant seal behaviour showed both that site fidelity increases with age (McMahon & Bradshaw 2004) and that more experienced females time their arrival more accurately (Carrick *et al.* 1962b). Older females should therefore have less need to move around during the breeding season, and less time to do so.

### **5.3.3 Breeding males and females**

The pattern shown by breeding males in number of times moved and the number of sites visited during the breeding haulout was very clear compared to the pattern shown by breeding females. The increase in number of times moved and number of sites visited with an increase in age of males can be explained by the fact that mature breeding males are experienced and are the most actively involved in competition for access to females (McCann 1983). There was a significant difference in behaviour between the sexes for corresponding ages as determined by all measures of movement, with males moving more often, visiting more sites and moving further than females. The relatively low frequency of movement shown by females was likely due to the fact that they need to be with dependent and relatively immobile pups for the most of the duration of the breeding season (Carlini *et al.* 2005), as well as reluctant to move due to the harassment of peripheral males (Galimberti *et al.* 2000b). During this period they tend to loose up to 40% percent of mass and 50% of body energy reserves (Fedak *et al.* 1996; Carlini *et al.* 2004). Males were able to move relatively more because they were not restricted to site, except for the minority that were beachmasters that were able to successfully defend their harems for the duration of the breeding season. These differences were also noted for the polygamous grey seals, where males showed a greater mobility at the breeding colony than females (Twiss *et al.* 1994). Elephant seal males also spend longer periods ashore than females; females begin to arrive 1-4 weeks later than the first males (Carlini *et al.* 2002). Furthermore, agonistic interactions between males encouraged the loser to move between sites, while bachelors may move in search of undefended harems. These movements happen in the latter stages of the breeding season when there is marked increase in the number of bachelors (Condy 1979; Bester 1990)

### **5.3.4 Moulting males**

Male elephant seals showed not a clear pattern in the number of times moved, number of sites visited and the distance moved during the moult haulout. The young adult males (6- and 7-year-olds) moved more often and visited more sites than both younger and older age classes. The significant differences between young adult males and both younger and older age classes may be the result of the difference in length of time the different elephant seals of different ages spend ashore. Since the younger adults were likely not successful in controlling harems during the previous breeding haulout, it may result in them hauling out earlier than mature breeders for the moult. Carrick *et al.* (1962a) also reported that at Macquarie Island the length of haulout during the

moult evidently increases with age, which is the case for the Marion Island population (Kirkman *et al.* 2003). In addition, 6- and 7-year-olds as young or immature breeders during the breeding season haulout, were largely unlikely to be successful in controlling harems and very few were probably involved in interactions competing for the access to cows. As a result they are likely to arrive for the moult haulout with more of their energy reserves intact than the mature males that have been fasting while involved in fighting for and controlling of harems. Therefore young adult males moved more, visited more sites and moved further than immatures and older adults.

### **5.3.5 Moulting females**

Female elephant seals of different age classes showed differences in terms of their moult haulout behaviour. Although the results were not consistent throughout the three measures of movement, younger (Y & SA) females differed significantly from the adult females. This was possibly as a result of the different obligations of these groups prior to the moult haulout. Most of the adult females were involved in the strenuous and energy taxing breeding haulout (Fedak *et al.* 1996; Carlini *et al.* 2004; Carlini *et al.* 2005) approximately two months earlier (Boyd *et al.* 1993; Carlini *et al.* 2005), whereas the younger or immature seals were involved in the clearly less demanding winter or resting phase. Therefore it conceivably resulted in young females moving more times, visiting more sites and moving further than adult females.

The other likely contributing factor to the significant difference between the adult and immature seals was the haul out site preference during the moult haulout. Wolf (2005) noted that habitat preferences vary within a species: sex and age classes can segregate in habitat use (Temeles & Kress 2003). Carrick *et al.* (1962a) observed that adult cows at Macquarie Island preferred to moult further inland, in the deeper wallows, than younger animals. It was thus possible that the presence of younger seals at moult sites closer to the beach front allowed them to change sites more often.

### **5.3.6 Moulting males and females**

Moulting elephant seals of both sexes showed similar patterns in haulout behaviour until age five, whereafter differences between males and females were apparent for all three measures of movement. This was possibly due to the differences in onshore obligations among older animals. The significant difference between males and females of all comparable ages except the underyearlings and seals older than 8 years was probably a result of difference in behaviour and

requirements for the previous haulout. The moulting process require protein to support growth of new integument and fat mobilisation for their metabolic needs (Carlini *et al.* 2005), but the energy reserves of adults are still somewhat depleted from the rigours of the previous breeding season (Fedak *et al.* 1996; Carlini *et al.* 2004; Carlini *et al.* 2005), while those of younger animals are not (since their previous haulout was a winter haulout). Male and female yearlings show few differences in behaviour and physical appearance (Carrick *et al.* 1962; McLaren 1993). Therefore the absence of difference in the movement of these animals is expected. The significant difference between males of different ages and all adult females ( $\geq 3$ -year-olds) are likely caused by the influence of the previous haulout. Adult females that participate in this moult haulout might not have re-gained their pre-breeding mass from the previous breeding haulout; and as a result of lower energy levels showed few intersite movements during this period.

There was no significant difference in number of times moved and number of sites visited between younger animals ( $\leq 2$ -year-olds), possibly because animals of this age group were not involved in the breeding haulout. The results showed no significant difference between the immature males ( $\leq 5$ -year-olds) and the younger females ( $\leq 3$ -year-olds) and this can be explained by the fact that males of this age were still immature and had not reached breeding status. Animals of all these age groups preferred to moult on the beaches (Carrick *et al.* 1962a) and therefore their behaviour was more likely to be the same during the moult haulout. This increased their opportunities of changing sites more often than the older animals that moult in the wallows. As a result, although the findings were not consistent throughout the ages, immature (yearlings & subadults) males visited significantly more sites and moved further overall than some older female of different ages. Older females prefer hauling out in the wallows for the moult as opposed to the younger or immature seals that prefer hauling out on the beaches (Carrick *et al.* 1962b). As a result, the moulting males age 3 to 7 years old (largely immature) moved significantly further than the moulting females of the same ages (largely mature) (Carrick *et al.* 1962a).

### **5.3.7 Wintering males**

Wintering male elephant seals showed a clear pattern in all three measures of movement, probably because during this period animals appear to sleep or are completely inactive for long periods (Carrick *et al.* 1962a). As was expected there was no significant difference in all three measures of movement among ages, because only immature individuals were involved in this haulout.

### **5.3.8 Wintering females**

Female elephant seals at Marion Island showed a clear pattern in the number of times moved, the number of sites visited and the distance moved during the winter haulout. There was no difference between ages because of similar obligations during this period. But the 1-year-olds moved more, visited more sites and moved further than all other females. This was a result of differences in participation level between yearling, underyearlings and sub-adult which resulted in more sample size for the yearlings. At Macquarie Island the proportion of individuals hauling out in the second year (1-year-olds) was higher than in their first year (Carrick *et al.* 1962a), which is similar to the findings by Kirkman *et al.* (2001) that participation levels of underyearlings is lower than that of yearlings of corresponding sex and than 3-year olds in the case of males at Marion Island.

### **5.3.9 Wintering males and females**

Male elephant seals showed clear patterns in all three measures of movement as compared to the females during the winter haulout. Generally all males moved more than all females during the winter haulout at Marion Island and as a result they visited more sites and moved further than all females. The underyearling males showed a significant difference to the 2-year old females in all three measures of movement, a likely result of earlier maturity in females. At Marion Island participation levels by male and females in the winter haulout declined before individuals hauled out in the breeding season or become pregnant (Kirkman *et al.* 2001). The 2-year old females were likely to be pregnant during the wintering haulout since many of them start pupping at the age of three at Marion Island (Bester & Wilkinson 1994). However, the significant difference between underyearling males and females in terms of the number of sites visited and distances moved was not as expected. These individuals were all in their first year of life and were expected to show similar behaviour, although Wilkinson and Bester (1990) found that male underyearlings moved more than underyearling females. One would rather have expected a significant difference between male and female yearlings and subadults. Kirkman *et al.* (2001) also found that participation in the winter phase differed between sexes, except among underyearlings, and that within each sex, both age and reproductive history influenced participation. Male underyearlings moved significantly further than females of the same age, and also the female underyearlings moved significantly further than all males.

## CHAPTER 6

### CONCLUSION

The results showed that, for both sexes of southern elephant seals, there is a clear pattern of movement during haulouts. There was an increase in frequency of number of times moved, sites visited and distance moved with an increase in age for males, while the opposite is true for females. This was likely because of different obligations of the different sexes as they age. All three factors; sex, age and haulout type, had an effect on the frequency of times moved, the number of sites visited and the distance moved. In most cases the null hypotheses were disproved for all three measures of movement. In terms of the frequency of times moved, sites visited and distance moved there was no sex bias in immature seals, very likely because at this stage of their life there are few marked behavioural differences between the sexes (Modig *et al.* 1995). Breeding adult males moved more frequently, visited more sites and moved further than elephant seals of all other age classes. Breeding adult females moved less frequently, visited fewer sites and moved less than elephant seals of all other age classes, because they had an obligation of taking care of pups during this period (Carrick *et al.* 1962a). There was very little difference in the frequency of number of times moved, sites visited and distance moved between different ages of breeding females, because during this period females have similar social ranks.

While a number of null hypotheses were disproved, fewer others were not. The differences in behaviour (in terms of movement between sites) between adult males and females, especially during the breeding season contrast with far less difference in behaviour between the sexes for immature animals. Older adult males moved further than younger adult males, likely because of changes in social rankings. The null hypothesis that behaviour does not change with age for female elephant seals was not disproved, likely because there was little change in social ranking with age, especially relative to adult males. The null hypotheses that behaviour of southern elephant seals hauling out for winter was not affected by age and sex was not disproved, likely because only immatures take part in this haulout and the different age and sex classes have similar obligations. Subadult elephant seals visited more sites than adult elephant seals during the moult, likely due to the influence of their previous haulout. Adult are conceivably exhausted from the energy taxing breeding haulout, while subadult were involved in the winter haulout or resting phase. The null hypotheses that behaviour of elephant seals does not change with haulout type was disproved, this was likely due to different obligations they have during different haulouts. The differences in

behaviour (in terms of movement between sites) between moulting immature and adult females, contrast with a far smaller difference in behaviour between age classes for males during the moult. The null hypotheses that behaviour does not differ between sexes during the moult was disproved. In the case of adults, it is likely that the obligation of the previous breeding haulout has had an influence. Adult males were involved in more fights to access the cows or to defend the harems. So males were more exhausted than females. The lack of any difference in movement when considering interactions between haulout types and ages classes is not surprising since these categories include both sexes and the substantial effect of sex class on movement has now been established.

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## APPENDICES

### APPENDIX 1: GLOSSARY

**Adult (A)** – Age class of females that have hauled out to breed, or males that have reached their sixth birthday.

**Assistant beachmaster (ABM)** – Adult male elephant seal controlling mating access to part of a harem that contains too many females for a single beachmaster to control access to at all times.

**Bachelor (B)** - Adult male elephant seal having hauled out during breeding season but not controlling mating access to at least two adult females.

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

**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.

**Challengers (CH)** – Adult male elephant seals not controlling mating access, but fighting with beachmaster for access to the females.

**Cohorts** – A group of individual animals of the same species born in the same area in the same year.

**Harem** – Social unit which is composed of a variable number of cows, their pups and a small number of bulls of varying social rank, one of which is dominant to all others.

**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 seals may haulout, and therefore be recorded at several sites.

**Haulout record (HOrecord)** - A single observation of a seal at one site on one day. A haulout record corresponds to a single row in the database.

**Haulout type (HOtype)** - Period ashore during which a seal engages in a specific type of behaviour, natal, moult, winter or breeding.

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

**Intersite movement** - The movement of any age class elephant seals between discrete beaches of the same location during one haulout event.

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

**Natal period** – The period where new born pups are ashore before their first extended foraging trip.

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

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

**Site** – Contiguous portion of coastline at which seals can haul out and which is separated from other sites by sections of the coastline that are inaccessible to seals.

**Subadult (SA)** – Age class of elephant seals that are between two and three years of age in the case of females, and in the case of males, have reached their second birthday but have not yet reached their seventh birthday.

**Underyearling (UY)** – Age class of seals resighted during the summer of their birth, and the following winter.

**Yearlings (Y)** - Age class of seals in their first year.

**Winter haulout (Resting Phase)** - Haulout during 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.

**Weaned pups** – Pups ashore during the breeding seasons that have finished their suckling period and are separated from their mothers.

## APPENDIX 2: POPULATIONS OF SOUTHERN ELEPHANT SEALS

**Table 1:** The three stocks of southern elephant seal population with their trends in Southern Ocean (SCAR EGS .2004)

| Stock                                  | Locality                           | Year of census | Trend in population abundance | Reference                         |  |
|--|------------------------------------|----------------|-------------------------------|-----------------------------------|--|
| <b>South Georgia</b>                   | South Georgia                      | 1995           | Stable                        | Boyd <i>et al.</i> (1996)         |  |
|  | South Orkney Islands               | 1985           | Uncertain                     | McCann (1985)                     |  |
|  | Bouvetoya                          | 1998           | Uncertain                     | Kirkman <i>et al.</i> (2000)      |  |
|  | Falkland Islands                   | 1960           | Uncertain                     | Laws (1960)                       |  |
|  | Sea Lion (Falklands)               |                | 2001                          | Stable                            | Galimberti <i>et al.</i> (2001), (pers.comm.)      |
|  |                                    |                | 2003                          | Declining                         | Galimberti (pers.comm.)                            |
|  | Gough Island                       | 1998           | Declining                     | Bester <i>et al.</i> (2001)       |  |
|  | King George Island                 |                | 1995                          | Declining                         | Vergani & Stanganelli (1990), Carlini (pers.comm.) |
|  |                                    |                | 1999<br>2003                  | Declining<br>Fluctuating          | Carlini (pers.comm.)<br>Carlini (pers.comm.)       |
|  | Nelson Island (Duthoit Point only) | 1985           | Uncertain                     | Vergani <i>et al.</i> (1987)      |  |
|  | Valdés Peninsula                   |                | 1982                          | Increasing                        | Vergani <i>et al.</i> (1987)                       |
|  |                                    |                | 1999                          | Increasing                        | Lewis <i>et al.</i> (1998), Lewis (pers.comm.)     |
| Livingston Island (Cape Shirreff only) |                                    | 2001           | Increasing                    | Lewis (pers. comm.)               |  |
|  |                                    | 2003           | Fluctuating                   | Goebel (pers.comm.)               |  |
| <b>Iles Kerguelen</b>                  | Marion Island                      | 1994           | Declining                     | Pistorius <i>et al.</i> (1999)    |  |
|  |                                    | 1997           | Declining                     | Pistorius <i>et al.</i> (1999)    |  |
|  |                                    | 1999           | Stable                        | Pistorius <i>et al.</i> (2004)    |  |
|  |                                    | 2003           | Increasing                    | McMahon <i>et al.</i> (In review) |  |

|                         |                          |      |                    |                                     |
|-------------------------|--------------------------|------|--------------------|-------------------------------------|
|                         | Heard Island             | 1985 | Declining          | Burton (1986), Slip & Burton (1999) |
|                         |                          | 1992 | Increasing?        | Slip & Burton(1999)                 |
|                         | Iles Kerguelen (Courbet) | 1977 | Declining          | Van Aarde (1980)                    |
|                         |                          | 1992 | Stable?            | Guinet <i>et al.</i> (1994)         |
|                         |                          | 1997 | Stable/increasing? | Guinet <i>et al.</i> (1999)         |
|                         | Iles Crozet (Possession) | 1976 | Declining          | Barrat & Mougin (1978)              |
|                         |                          | 1992 | Decreasing         | Guinet <i>et al.</i> (1992)         |
|                         |                          | 1997 | Stable             | Guinet <i>et al.</i> (1999)         |
| <b>Macquarie Island</b> | Macquarie Island         | 1985 | Declining          | Hindell & Burton (1987)             |
|                         |                          | 1997 | Declining          | Burton (pers.comm.)                 |
|                         |                          | 2003 | Increasing         | Burton (pers. comm.)                |
|                         | Campbell Island          | 1986 | Declining          | Taylor & Taylor (1989)              |
|                         | Antipodes Island         | 1978 | Uncertain          | Taylor & Taylor (1989)              |

**APPENDIX 3: NUMBER OF MALE AND FEMALE ELEPHANT SEALS OF DIFFERENT AGE CLASSES, HAULOUT TYPES OBSERVED FOR ALL THREE MESUASURES OF MOVEMENT**

**Table 2:** Number (N) of male and female elephant seals of different age classes observed, and the mean and maximum number of moves made at Marion Island.

| Class | N    |      | Mean |      | Standard Deviation |      | Maximum |   |
|-------|------|------|------|------|--------------------|------|---------|---|
|       | M    | F    | M    | F    | M                  | F    | M       | F |
| UY    | 1918 | 2099 | 0.25 | 0.21 | 0.54               | 0.51 | 3       | 3 |
| Y     | 2256 | 2384 | 0.30 | 0.28 | 0.56               | 0.55 | 3       | 4 |
| SA    | 3827 | 1449 | 0.36 | 0.27 | 0.64               | 0.55 | 4       | 3 |
| A     | 519  | 5123 | 0.81 | 0.20 | 1.15               | 0.48 | 7       | 3 |

**Table 3:** Number (N) of male and female elephant seals observed during different haulout types, and the mean and maximum number of moves made at Marion Island.

| Haulout type | N    |      | Mean |      | Standard Deviation |      | Maximum |   |
|--------------|------|------|------|------|--------------------|------|---------|---|
|              | M    | F    | M    | F    | M                  | F    | M       | F |
| Natal        | 1338 | 1502 | 0.24 | 0.21 | 0.56               | 0.53 | 3       | 3 |
| Winter       | 2938 | 1934 | 0.30 | 0.23 | 0.55               | 0.48 | 4       | 3 |
| Moult        | 3963 | 5420 | 0.37 | 0.26 | 0.65               | 0.55 | 4       | 4 |
| Breeding     | 281  | 2199 | 1.01 | 0.15 | 1.31               | 0.41 | 7       | 3 |

**Table 4:** Number (N) of seals of different age classes observed during different haulout types, and the mean and maximum number of moves made by elephant seals at Marion Island.

| Haulout type | Age Class | N    | Mean | Standard Deviation | Maximum |
|--------------|-----------|------|------|--------------------|---------|
| Natal        | 10        | 2840 | 0.22 | 0.55               | 3       |
| Winter       | 10        | 1177 | 0.25 | 0.47               | 3       |
|              | 20        | 2141 | 0.27 | 0.53               | 3       |
|              | 30        | 1554 | 0.29 | 0.55               | 4       |
| Moult        | 20        | 2499 | 0.30 | 0.57               | 4       |
|              | 30        | 3722 | 0.35 | 0.64               | 4       |
|              | 40        | 3162 | 0.26 | 0.56               | 4       |
| Breeding     | 40        | 2480 | 0.25 | 0.64               | 7       |

**Table 5:** Number (N) of male and female elephant seals of different age classes observed, and the mean and maximum number of sites visited at Marion Island.

| Class     | N    |      | Mean |      | Standard Deviation |      | Maximum |   |
|-----------|------|------|------|------|--------------------|------|---------|---|
|           | M    | F    | M    | F    | M                  | F    | M       | F |
| <b>UY</b> | 1918 | 2099 | 1.22 | 1.18 | 0.45               | 0.41 | 4       | 4 |
| <b>Y</b>  | 2256 | 2384 | 1.27 | 1.26 | 0.50               | 0.48 | 4       | 4 |
| <b>SA</b> | 3827 | 1449 | 1.32 | 1.24 | 0.53               | 0.48 | 4       | 4 |
| <b>A</b>  | 519  | 5123 | 1.64 | 1.18 | 0.86               | 0.41 | 5       | 4 |

**Table 6:** Number (N) of male and female elephant seals observed during different haulout types, and the mean and maximum number of sites visited at Marion Island.

| Haulout type    | N    |      | Mean |      | Standard Deviation |      | Maximum |   |
|-----------------|------|------|------|------|--------------------|------|---------|---|
|                 | M    | F    | M    | F    | M                  | F    | M       | F |
| <b>Natal</b>    | 1338 | 1502 | 1.19 | 1.17 | 0.43               | 0.41 | 4       | 4 |
| <b>Winter</b>   | 2938 | 1934 | 1.28 | 1.22 | 0.50               | 0.43 | 4       | 3 |
| <b>Moult</b>    | 3963 | 5420 | 1.32 | 1.23 | 0.54               | 0.47 | 4       | 4 |
| <b>Breeding</b> | 281  | 2199 | 1.78 | 1.14 | 0.95               | 0.36 | 5       | 3 |

**Table 7:** Number (N) of seals of different age classes observed during different haulout types, and the mean and maximum number of sites visited by elephant seals at Marion Island.

| Haulout type    | Age Class | N    | Mean | Standard Deviation | Maximum |
|-----------------|-----------|------|------|--------------------|---------|
| <b>Natal</b>    | UY        | 2840 | 1.18 | 0.42               | 4       |
| <b>Winter</b>   | UY        | 1177 | 1.24 | 0.45               | 3       |
|                 | Y         | 2141 | 1.25 | 0.48               | 4       |
|                 | SA        | 1554 | 1.27 | 0.49               | 4       |
| <b>Moult</b>    | Y         | 2499 | 1.27 | 0.50               | 4       |
|                 | SA        | 3722 | 1.31 | 0.53               | 4       |
|                 | A         | 3162 | 1.23 | 0.48               | 4       |
| <b>Breeding</b> | A         | 2480 | 1.21 | 0.51               | 5       |

**Table 8:** Number (N) of male and female elephant seals of different age classes observed, and the mean and maximum distance travelled at Marion Island.

| Class | N    |      | Mean |      | Standard Deviation |      | Maximum |       |
|-------|------|------|------|------|--------------------|------|---------|-------|
|       | M    | F    | M    | F    | M                  | F    | M       | F     |
| UY    | 1918 | 2099 | 1.34 | 0.98 | 4.92               | 4.61 | 50.03   | 86.70 |
| Y     | 2256 | 2384 | 1.75 | 1.67 | 5.75               | 5.83 | 77.93   | 86.70 |
| SA    | 3827 | 1449 | 1.63 | 1.33 | 4.94               | 4.94 | 100.23  | 72.63 |
| A     | 519  | 5123 | 2.43 | 0.91 | 5.64               | 4.12 | 61.80   | 91.92 |

**Table 9:** Number (N) of male and female elephant seals observed during different haulout types, and the mean and maximum distance travelled at Marion Island.

| Haulout type | N    |      | Mean |      | Standard Deviation |      | Maximum |       |
|--------------|------|------|------|------|--------------------|------|---------|-------|
|              | M    | F    | M    | F    | M                  | F    | M       | F     |
| Natal        | 1338 | 1502 | 1.02 | 0.92 | 4.52               | 4.80 | 50.03   | 86.70 |
| Winter       | 2938 | 1934 | 1.59 | 1.33 | 5.18               | 4.87 | 61.40   | 58.12 |
| Moult        | 3963 | 5420 | 1.81 | 1.30 | 5.90               | 5.05 | 100.23  | 91.92 |
| Breeding     | 281  | 2199 | 2.92 | 0.73 | 5.85               | 3.72 | 52.20   | 73.35 |

**Table 10:** Number (N) of elephant seals of different age classes observed during different haulout types, and the mean and maximum distance travelled at Marion Island.

| Haulout type | Age Class | N    | Mean | Standard Deviation | Maximum |
|--------------|-----------|------|------|--------------------|---------|
| Natal        | UY        | 2840 | 0.97 | 4.67               | 86.70   |
| Winter       | UY        | 1177 | 1.60 | 4.98               | 42.14   |
|              | Y         | 2141 | 1.67 | 5.79               | 61.40   |
|              | SA        | 1554 | 1.15 | 3.92               | 42.43   |
| Moult        | Y         | 2499 | 1.74 | 5.80               | 86.70   |
|              | SA        | 3722 | 1.72 | 5.87               | 100.23  |
|              | A         | 3162 | 1.10 | 4.49               | 91.92   |
| Breeding     | A         | 2480 | 0.98 | 4.08               | 73.35   |

## APPENDIX 4: EXAMPLES OF COLLECTED DATA FOR INDIVIDUALS

**Table 11:** Details of all haulout events for the male elephant seal, *Mirounga leonina*, tag number OB 0316, at Marion Island. Details given are: Age = age at which each haulout event took place, HOtype = Haulout type, N record = number of times the seal was recorded during that haulout event, N site = number of sites that were visited, and N moves = number of times moved.

| Age | HOtype   | Nrecord | Nsite | Nmoves | Distance moved (km) |
|-----|----------|---------|-------|--------|---------------------|
| 0   | Natal    | 4       | 1     | 0      | 0                   |
| 1   | Moult    | 4       | 1     | 0      | 0                   |
| 2   | Moult    | 2       | 1     | 0      | 0                   |
| 2   | Winter   | 1       | 1     | 0      | 0                   |
| 3   | Moult    | 4       | 1     | 0      | 0                   |
| 4   | Winter   | 5       | 1     | 0      | 0                   |
| 5   | Moult    | 5       | 2     | 1      | 8.1                 |
| 5   | Winter   | 2       | 1     | 0      | 0                   |
| 6   | Moult    | 6       | 1     | 0      | 0                   |
| 7   | Breeding | 1       | 1     | 0      | 0                   |
| 7   | Moult    | 3       | 2     | 2      | 2.8                 |
| 8   | Breeding | 4       | 1     | 0      | 0                   |
| 8   | Moult    | 5       | 4     | 3      | 14.9                |
| 9   | Breeding | 4       | 3     | 2      | 4.4                 |
| 9   | Moult    | 2       | 1     | 0      | 0                   |
| 10  | Breeding | 1       | 1     | 0      | 0                   |
| 10  | Moult    | 3       | 1     | 0      | 0                   |
| 11  | Breeding | 14      | 1     | 0      | 0                   |

**Table 12:** Details of all haulout events for the female elephant seal, *Mirounga leonina*, tag number OB 0032, at Marion Island. Details given are: Age = age at which each haulout event took place, HOtype = Haulout type, N record = number of times the seal was recorded during that haulout event, N site = number of sites that were visited, and N moves = number of times moved.

| Age | HOtype   | Nrecord | Nsite | Nmoves | Distance moved (km) |
|-----|----------|---------|-------|--------|---------------------|
| 0   | Natal    | 4       | 1     | 0      | 0                   |
| 0   | Winter   | 1       | 1     | 0      | 0                   |
| 1   | Moult    | 3       | 3     | 2      | 0.8                 |
| 1   | Winter   | 2       | 2     | 1      | 0.8                 |
| 2   | Moult    | 3       | 1     | 0      | 0                   |
| 2   | Winter   | 2       | 1     | 0      | 0                   |
| 3   | Moult    | 2       | 1     | 0      | 0                   |
| 4   | Moult    | 5       | 1     | 0      | 0                   |
| 5   | Breeding | 2       | 1     | 0      | 0                   |
| 5   | Moult    | 1       | 1     | 0      | 0                   |
| 6   | Breeding | 3       | 1     | 0      | 0                   |
| 6   | Moult    | 3       | 1     | 0      | 0                   |
| 7   | Moult    | 4       | 1     | 0      | 0                   |
| 9   | Breeding | 2       | 1     | 0      | 0                   |
| 10  | Moult    | 1       | 1     | 0      | 0                   |
| 11  | Breeding | 2       | 1     | 0      | 0                   |
| 11  | Moult    | 1       | 1     | 0      | 0                   |

**APPENDIX 5: THE GLM PROCEDURE RESULTS**

**Table 13:** ANOVA (SAS, Procedure GLM) analysis of Southern elephant seals at Marion Island determining the influence of sex, age class, haulout type and their interactions to the distance moved.

| Source                    | DF | Type I SS | Mean Square | F Value | Pr > F  |
|---------------------------|----|-----------|-------------|---------|---------|
| Sex                       | 1  | 109.58    | 109.59      | 110.91  | <. 0001 |
| Class                     | 3  | 21.84     | 7.28        | 7.37    | <. 0001 |
| Sex* Class                | 3  | 72.94     | 24.31       | 24.61   | <. 0001 |
| Haulout type              | 3  | 26.24     | 8.75        | 8.85    | <. 0001 |
| Sex (Haulout type)        | 3  | 12.89     | 4.30        | 4.35    | 0.0046  |
| Class (Haulout type)      | 1  | 1.36      | 1.36        | 1.37    | 0.2414  |
| Sex* Class (Haulout type) | 1  | 0.03      | 0.03        | 0.03    | 0.8639  |

**Table 14:** ANOVA (SAS, Procedure GLM) analysis of Southern elephant seals at Marion Island determining the influence of sex, age class, haulout type and their interactions to the number of sites visited.

| Source                    | DF | Type I SS | Mean Square | F Value | Pr > F  |
|---------------------------|----|-----------|-------------|---------|---------|
| Sex                       | 1  | 117.34    | 117.34      | 119.48  | <. 0001 |
| Class                     | 3  | 42.70     | 14.23       | 14.49   | <. 0001 |
| Sex* Class                | 3  | 149.67    | 49.89       | 50.80   | <. 0001 |
| Haulout type              | 3  | 22.68     | 7.56        | 7.70    | <. 0001 |
| Sex (Haulout type)        | 3  | 25.54     | 8.51        | 8.67    | <. 0001 |
| Class (Haulout type)      | 1  | 3.56      | 3.56        | 3.63    | 0.0568  |
| Sex* Class (Haulout type) | 1  | 1.22      | 1.22        | 1.25    | 0.2642  |

**Table 15:** ANOVA (SAS, Procedure GLM) analysis of Southern elephant seals at Marion Island determining the influence of sex, age class, haulout type and their interactions to the number of moves made.

| <b>Source</b>                    | <b>DF</b> | <b>Type I<br/>SS</b> | <b>Mean<br/>Square</b> | <b>F Value</b> | <b>Pr &gt; F</b> |
|----------------------------------|-----------|----------------------|------------------------|----------------|------------------|
| <b>Sex</b>                       | 1         | 111.24               | 111.24                 | 113.28         | <. 0001          |
| <b>Class</b>                     | 3         | 38.56                | 12.85                  | 13.09          | <. 0001          |
| <b>Sex* Class</b>                | 3         | 153.22               | 51.07                  | 52.01          | <. 0001          |
| <b>Haulout type</b>              | 3         | 15.68                | 5.23                   | 5.32           | <. 0012          |
| <b>Sex (Haulout type)</b>        | 3         | 40.90                | 13.63                  | 13.88          | <. 0001          |
| <b>Class (Haulout type)</b>      | 1         | 3.89                 | 3.89                   | 3.96           | 0.0465           |
| <b>Sex* Class (Haulout type)</b> | 1         | 0.01                 | 0.01                   | 0.01           | 0.9334           |